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A STUDY OF SOME WOOD CHARACTERS OF *Pinus caribaea* Morelet var. *hondurensis* Barr. and Golf.: THEIR VARIATION, ASSOCIATION, AND COVARIATION WITH TREE GROWTH AND SOME FACTORS OF THE ENVIRONMENT

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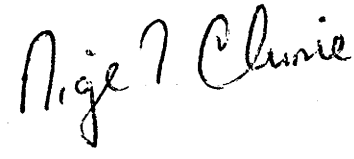
Except where acknowledged otherwise, the content of this thesis reports my original work.



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ABSTRACT

A detailed study is presented of the variation of wood density features (measured by X-ray densitometry) and of wood cell dimensions in twenty 18-year old trees of *Pinus caribaea* Morelet var. *hondurensis* Barr. and Golf., from a routine planting at Beerburrum in southern coastal Queensland (27° S).

The inter-relationships among the complex of wood characters is examined: The technique of principal component analysis is used to identify and to estimate these inter-relationships, and to simplify the apparent dimensionality of variation and covariation in the complex data sets. The results provide an effective basis for hypothetical inference; and the variation among a large number of wood characters is effectively summarised, i.e., expressed in a reduced number of dimensions.

The patterns and extent of variation of the wood characters within trees are examined, and differences in these features of structural development between trees made evident. Very substantial phenotypic variation is encountered.

The effect of sample height upon the estimate of whole-tree values of the wood characters is examined: The relationships between the mean values determined from samples taken at a given level (breast height, 10%, 20%, 40%, 60%, and 80% of tree height) and the mean tree estimate are presented; and it is shown that mean estimates derived from measures of the stem cross-section at any given level to 60% of the tree height are representative of whole-tree values and, thus, facilitate valid between-tree comparison.

An estimate is made of the effects upon the wood characteristics of radial growth rate and of position within the stem. The variation of the densitometric characters and the closely associated variation of lumen width and wall thickness of the latewood tracheids is shown to be independent of the effects of radial growth rate, but

strongly associated with radial and axial position effects. The lumen and cell widths of earlywood tracheids are not affected by position within the stem, and, together with the width of the intra-incremental latewood zone and the associated cell width of the latewood tracheids, are strongly influenced by radial growth rate.

The nutritional status of the soil and foliage is examined. The inter-relationships between individual nutrient factors and complexes of inter-related factors in the soil and foliage are identified and estimated; and an estimate is made of the relationships between nutritional features of the soil and foliage and the wood characteristics of the trees. A moderately strong relationship between foliage nutrient levels and the lumen and cell widths of the tracheids is identified and characterised.

The variation of the densitometric characteristics of the wood of trees growing at varying altitude in tropical north Queensland (17° S) is summarised in an annex to the thesis, and the results alluded to in comparative discussion.

Very pronounced phenotypic differences in wood characteristics are encountered between trees growing under similar conditions and between stands established on sites of diverse ecology.

SUMMARY

A study is presented of selected wood characters of trees of Pinus caribaea var.hondurensis from an 18-year old plantation in southern coastal Queensland.

1. Twenty trees were selected by ranked-set sampling (Chapter 2), ranking on diameter at breast height. Wood discs were removed from each tree at breast height (1.3m) and percentile height levels (10%,20%,40%,60%,80%). Samples of expanded leaves were taken from the penultimate growth whorl and topsoil cores from near the base of each tree for an examination of the nutritional status of the foliage and soil (for sample preparation and analytical procedures see Appendix 2).

2. From each wood disc a strip was cut across the diameter with the most symmetric radii to yield a sample (2 radii x 6 height levels in 20 trees) for the study of the structural features of the wood.

3. A comprehensive range of densitometric features (wood maximum, minimum, and mean density; density range; latewood percentage; width of the latewood zone; ring width; latewood ratio) and anatomical characteristics (radial double-wall thickness, lumen and cell widths of tracheids in the earlywood and latewood zones; tracheid length in the earlywood) in each of the annual growth increments was examined.

4. Wood densitometric features were measured using the technique of X-ray densitometry (described in Section 3.1.). Prior to irradiation, the wood samples each were extracted in benzene:ethanol (1:2), machined to a thickness of 6.9 ± 0.04mm in the radial longitudinal plane, and conditioned to 8 ± 0.5 percent moisture content. Two

cellulose acetate calibration standards (step wedges) were irradiated with the wood samples on each film to facilitate the transformation of optical density to wood density values.

A Joyce-Loebl Mark III C.S. dual beam recording microdensitometer was used to translate the variation in optical contrast of the sample images on the X-ray film into continuous chart recordings. Mean density was estimated using an electronic integrator. All other measures from the chart recordings were made by hand. Transformation of optical density measures to wood density estimates by polynomial interpolation was performed by electronic computer. Latewood percentage was measured as the proportion of the annual increment with a density greater than 0.468. The wood density features were measured in each annual growth ring (8 characters x 2402 sample locations).

5. The measurement of wood cell dimensions is described in Section 3.2. Measures were made in the third, seventh, and eleventh annual growth ring (measured from the bark) in one radius at each of the six height levels in which these rings occur (see Section 4.2.b).
i). Tracheid length: Earlywood tissues were macerated and separated by high-frequency vibration, and the projected images (magnified x45) of 50 unbroken tracheids (25 tracheids in each of 2 slides per sample unit) were measured on a screen using a map tracing wheel.
ii). Tracheid radial double-wall thickness and lumen diameter: Measured to a precision of 0.5 microns per measure on the reflected images (magnified x 687.5) using a Leitz Ultrapack reflection microscope mounted on a dual linear traverse measuring micrometer. 50 cells from at least six radial files were measured in each of the earlywood and latewood zones of the selected growth rings.

6. The association between wood characters was examined by simple correlation analysis (Section 4.2.). There is a high degree of intercorrelation among the wood characters. Intercorrelation among the densitometric characters other than the latewood ratio is of a high order. The very strong correlation ($r = 0.87$ to 0.89) of wood mean density with latewood percentage indicates that mean density may be predicted with a high degree of precision from measures of latewood

percentage. The intraincremental density range is almost completely correlated (r = 0.98)with ring maximum density.

Tracheid dimensions, excepting the lumen and cell widths of tracheids in the earlywood, are, in general, highly correlated with the densitometric characters. These intercorrelations are of a particularly high order with double-wall thickness and lumen diameter of latewood tracheids.

There is a close association between the width of the annual growth ring and each of the densitometric characters other than the latewood ratio and the width of the intraincremental latewood zone. Ring width is significantly correlated with cross-sectional dimensions of the latewood tracheids and with the tracheid length (and to a lesser extent double-wall thickness) of the earlywood tracheids but has no affinity with lumen or cell width of the earlywood tracheids.

The matrix of intercorrelations between characters is an important step in characterising the structural features of the wood but it is complex and difficult to interpret and introduces no generalisations in relation to the overall variation in the data set.

7. A multivariate model, principal component analysis (described in Appendix 1), was used to identify and estimate the interrelationships among the complex of wood characters. The results of the analyses, and the inference and conclusions derived from them, are presented in Section 4.2.

a). The principal component technique effected an efficient summary of the variation and covariation in the character complex. The effective dimensionality of variation in the measured densitometric and anatomical features was reduced from 15 to 3 dimensions (components) each of which was interpreted in terms of statistically independent linear combinations of the original 15 variables. The major component of variation accounts for nearly 50% of the variance of the standardised measures. It is highly correlated with each of the characters' ring mean density, ring maximum density, and latewood percentage; any of which could determine the component. Lumen or cell width of the earlywood tracheids can effectively determine the second component, which accounts for almost 20% of the variation. The third component, which accounts for 12% of the variation, could

be determined by either the width of the intraincremental latewood zone or the latewood ratio. The measure of one of these important variables from each of the three components would be required to describe effectively the variation of the densitometric and anatomical characteristics of the wood. Ring mean density alone effectively describes almost 50% of the variation.

b). The identification and estimation of relationships among the wood characters provided an effective basis for hypothetical inference of possible causal mechanisms underlying these relationships.

The first component is associated positively with the densitometric characters other than the latewood ratio, with which it has no affinity. It is strongly correlated with the contrast between latewood percentage and ring width. The component is strongly correlated with the contrast between wall thickness and lumen diameter of the latewood tracheids, but the affinity of the component with the latewood tracheid width is low to moderate. Earlywood tracheid wall thickness has its highest loading on the first component, but the correlation is relatively weak. Lumen and cell width of earlywood tracheids each have a low to negligible affinity with the first component. The loading of the component on tracheid length is high. These interrelationships are interpreted as:

i). The amount of cell wall material per unit volume of wood (i.e., proportion of wall material to void) in the intraincremental latewood zone is the anatomical characteristic that most influences the variation in the absolute values of the densitometric features of the wood, and in particular ring mean density and latewood percentage: width of the latewood tracheids has considerably less influence, but the larger diameter latewood tracheids tend to have wider lumens and thinner walls.

ii). The close association of ring mean density and latewood percentage and their contrast with ring width could result, to some degree, from the influence of annual growth rate on the relative proportion of thick-walled 'latewood' tissue in the growth ring: but the relationship might be a response to the effect of position in the stem cross-section.

iii).The very strong association of ring maximum density with the contrast of wall thickness and lumen width in the latewood is a cause-and-effect response of maximum density to the relative

proportion of wall material and void in the latewood tissues.
iv). The close association of ring minimum density with the latewood cell characteristics results from a common response to a position effect.
v). The common association of earlywood tracheid wall thickness and ring minimum density with the first component could be an expression of direct causal effect. The low affinity of the lumen width and cell diameter of the earlywood tracheids suggests that these anatomical characteristics have less influence than wall thickness on the lowest density values in the earlywood.
vi). Intraincremental density range tends to be greatest simultaneously with the highest values of both maximum and minimum density: It is most strongly influenced by changes in the value of maximum density.
vii).The close affinity of earlywood tracheid length with the first component may reflect, to some extent, collinearity in the variation of many of the variables with position in the stem cross-section. The strong correlation of the first component with the contrast of tracheid length and ring width and the high zero-order negative correlation of ring width and tracheid length may reflect a response of variation of tracheid length to growth rate.

The second component is characterised by the very high loadings on lumen width and cell diameter of the earlywood tracheids. Latewood tracheid width has its highest loading on this component, but the correlation is relatively weak. Latewood ratio and ring minimum density have low to moderate affinity with the second component: The correlation of the component with each of the other densitometric characters is weak or negligible. The second component represents a major aspect of variation among the wood character measures associated with the widths of the wood cells, particularly the earlywood tracheids (and lumen widths, which largely determine the overall C.S. diameter of the earlywood tracheids). This variation is largely independent (in a statistical sense) of the variation of the densitometric characters other than the latewood ratio. By inference, the width of the wood cells, although representing a large element of the overall variation in the wood, have little influence upon its densitometric features.

The third component is characterised by high loadings on latewood ratio, width of the intraincremental latewood zone, and

latewood tracheid diameter. The component represents an element of variation in the latewood characteristics that is largely independent (in a statistical sense) of the variation of the absolute values of the densitometric characteristics of the wood and of the earlywood anatomy. The variation is expressed as a positive association of the latewood tracheid C.S. size and indices of intraincremental latewood distribution and extent.

8. The extent and the patterns of variation of the densitometric characters maximum, minimum, and mean density, latewood percentage, and ring width within and between annual growth increments in the stem of each of the 20 trees was examined (Section 4.3.1.) : The results are summarised in 9. to 12. below.

9. Variation of wood density outward from the pith (Section 4.3.11.): Within the stem there is a central core of juvenile wood of relatively light texture and low density (but generally not less than 0.4 g/cc extracted density), which extends from the pith to the sixth or eighth growth ring over the height range: Distal to this central core the wood is of relatively uniform strong texture and high density. This feature of structural development is most strongly related to the pattern of development with age of latewood characteristics (latewood percentage; maximum density and associated intraincremental density range; and the wall thickness (increase) and lumen diameter (decrease) of latewood tracheids).

i). Ring maximum density is low (0.49 - 0.55) in the innermost one to three rings at each height level within the stem, but increases rapidly over the inner four to seven rings to very high values (0.80 +). The whole-ring mean density is relatively low (less than 0.5) in the inner six to eight rings. Ring minimum density is also uniformly lowest in the innermost approximately eight rings.

ii). Latewood is relatively poorly developed in the rings of the central core (ring values less than 30%). Within individual trees latewood is poorly developed or even absent altogether between one and four growth layers from the pith. Thereafter (varying from the second to the fifth growth layer) latewood is well developed.

iii). Relatively high values of ring width (generally in excess of 6mm for pooled tree means) are encountered in the inner core of 7 or 8 growth increments. Because radial growth rate during the period corresponding with corewood formation is relatively great the central core is of considerable extent and this feature of structural development could give rise to problems of seasoning degrade and variable strength properties caused by the inclusion of juvenile and mature wood in sawn material.

iv). Within the central core the pattern of systematic variation outwards from the pith of each of the densitometric characters changes with height in the tree : The general trends of change with height are similar with each of the characters maximum, minimum and mean density and latewood percentage. There is a linear increase outward from the pith in the lower bole (breast height to 10% of total tree height); in the central stem (20% to 60% of total height) there is an initial decrease (over 2 to 3 rings) followed by a linear increase; and an overall linear increase in the upper stem (80% of total tree height).

v). Distal to the central core there is a systematic linear trend of increase in the value for each of the characters maximum, minimum and mean density and latewood percentage. This trend shows no sign of approaching a maximum value by the 15th (outermost) ring laid down at tree age 18 years.

vi). The variability between adjacent growth layers in the values of maximum density and latewood percentage are quite pronounced: the year-by-year fluctuations in mean density and minimum density are, respectively, moderate and low.

vii). The variability between adjacent growth layers, particularly in the values of maximum density and latewood percentage, is most pronounced in the wood distal to the 'juvenile' core, and is of a relatively low order within the central core. This evidence suggests that the response of latewood characteristics during the period corresponding with 'corewood' formation is determined to a greater degree by inherent patterns of change in the physiological environment of wood formation associated with proximity to the stem apex and terminal meristems of the lateral shoots and the source of photosynthate (i.e., 'age' effects), and is less subject to the influence of the external environment than is the response of

latewood characteristics of the wood formed distally to the inner core.

viii). In most growth layers there is a single distinct major zone of latewood formation, but the occurrence of several narrow bands of latewood separated by wood of low density ('false rings') within an annual increment is not uncommon. The pattern of 'false ring' development is consistent within a growth layer over the height range within trees, and a generally similar pattern is evident between trees.

ix). The pattern of variation of ring width outward from the pith changes with height. In the lower stem (to 10% of tree height) ring width fluctuates about a relatively high value (6.8 - 9.4mm) in the innermost 5 or 6 rings : Distally there is a linear trend of decrease in ring width. Higher in the stem ring width tends to increase initially.

10. The variation with height of the weighted estimates of maximum, minimum and mean density of the stem cross-section in each of the 20 trees was examined in Section 4.3.12.1.

i). Minimum density: There is only slight variation with height of minimum density within trees: In most trees the trend is one of linear constancy of minimum density with height. For the pooled mean tree estimate there is a slight linear decrease from 0.364 at breast height to 0.342 at 80% of tree height. (mean whole-tree estimate 0.347).

ii). Mean density: Phenotypic differences between trees in the patterns of variation of mean density are more diverse. There is no constant systematic trend between trees associated with the absolute value of mean density. The range of variation within trees and between trees is greater than for minimum density. The pooled mean tree estimate shows a systematic linear decrease with height (0.538 at breast height to 0.457 at 80% : mean whole-tree estimate 0.495).

iii). Maximum density: The patterns of variation of maximum density with height are highly variable between trees: There is no constant systematic trend between trees associated with differences in the absolute value of maximum density. There are pronounced phenotypic differences between trees in the within-tree range of

maximum density, and between-tree differences in the absolute value of this character are of a high order. The pooled mean tree estimate shows a linear decrease with height (0.859 at breast height to 0.725 at 80% : mean whole-tree estimate 0.798).

11. The variation of wood density with height within an annual growth sheath: The variation with height of the densitometric characters within the third growth layer from the bark in each of the 20 trees was examined in Section 4.3.12.2.

i). Minimum density: There is considerable variation between trees both in the absolute value of minimum density at a given level and in the pattern of variation of minimum density with height. The pooled estimate for all trees shows a low-order linear decrease of minimum density with height (0.389 at breast height to 0.342 at 80%).

ii). Mean density: There are large differences between trees in the absolute value of mean density at a given level within the growth sheath. There is a general decrease of mean density with height in individual trees, but pronounced phenotypic differences between trees are evident in the patterns of variation of mean density with height. The pooled estimate for all trees shows a moderate linear decrease with height (0.574 at breast height to 0.402 at 80%).

iii). Maximum density: There are very large phenotypic differences between trees in the absolute value of maximum density at a given level within the growth sheath (e.g., range 0.64 or 83% of the pooled average value of 0.77 at 40% of tree height); the differences being less pronounced at 80% of tree height. The patterns of variation with height are highly variable between trees. There is usually a marked decrease in the value of maximum density between 60% and 80% of tree height. There are pronounced phenotypic differences between trees in the range of maximum density within the growth sheath. The pooled mean estimate shows a decreasing linear trend with height to 60% of tree height (0.900 at breast height to 0.664 at 60%), and a more pronounced decrease from 60% to 80% (0.497).

iv). The patterns of variation of wood mean and minimum density

show no consistent relationship with the measured limits of the live crown. There is a more consistent marked depression in the value of maximum density in the region of the live crown (60% to 80% of total tree height), which is suggestive of crown association.

v). The width of the growth layer shows a systematic increase with height which is most pronounced in the upper stem from 40% to 80% of tree height (5.42mm at breast height to 6.02mm at 40% and 9.82mm at 80%).

vi). Latewood percentage shows a marked linear decrease with height within the growth layer (from 55.1% at breast height to 6.9% at 80% of tree height).

12. The variation of density features of the sheath of wood laid down annually was examined in each of the 20 trees (Section 4.3.13.).

i). Maximum density: There are pronounced phenotypic differences between trees in the pattern of variation with age of the weighted whole-sheath value of wood maximum density and in the absolute value of maximum density of corresponding growth sheaths. Trends of variation are highly variable between trees in the young stem (to tree age approximately 8 years). Thereafter there is an essentially linear, though highly irregular, trend of increase of sheath maximum density with age in all the more vigorous trees. In 5 of the least vigorous trees there is a quadratic trend of increase of sheath maximum density to a maximum value followed by a decrease : This quadratic trend is more pronounced, and the maximum value is reached at an earlier age in the more highly suppressed trees.

There are marked differences between trees in the rate of increase of sheath maximum density with age and these differences are not related to tree vigour; i.e., the pattern is highly variable between trees of comparable vigour.

The variability in the value of maximum density between adjacent growth layers is pronounced : An element of similarity of response between trees in some years is evident, but the response is highly variable between trees in many of the corresponding annual growth sheaths, particularly the inner sheaths.

There is a linear, though highly irregular, trend of increase in the pooled average estimate of whole-sheath maximum density with age.

ii). Minimum density: The variation with age of the weighted whole-sheath value of minimum density is relatively minor : minimum density remains almost constant with age in most trees. In some trees there is a systematic increase in sheath minimum density with age; this trend being most pronounced in the outer sheaths of trees of low vigour. There is no consistent trend of variation of minimum density in the inner sheaths. Variability between adjacent growth layers is relatively minor.

The range of difference between trees in whole-sheath minimum density at a given age is a considerable portion of the mean value.

The pooled average estimate of whole-sheath minimum density remains constant (0.33) to tree age 11 years, then increases (to 0.37 at age 17 years).

iii).Mean density: There are considerable differences between trees in the pattern of variation with age of whole-sheath mean density, and in the mean density of corresponding growth sheaths. Trends of variation in the inner sheaths, to age approximately 8 years, are highly variable : Thereafter there is a general linear increase in mean density with sheath age; the rate of increase being highly variable between trees.

Fluctuations in the value of whole-sheath mean density from year to year are considerable. Some of the annual fluctuations are consistent between trees, reflecting an element of consistency of response of trees to environmental change.

The variation with age of whole-tree mean density is highly variable between trees in the young stem. From an age of about 8 years there is a general linear increase of whole-tree mean density with tree age.

The pooled average estimate of whole-sheath mean density remains relatively constant (0.42) with age to 9 years : Thereafter there is a linear trend of increase with age (maximum 0.53). The pooled estimate of whole-tree mean density shows a similar trend from 0.42 (tree age 4 years) to 0.49 (18 years).

13. The variation of the average tracheid radial cross-sectional dimensions (wall thickness and lumen width of earlywood and latewood cells) of the stem cross-section with height in each of the 20 trees

was examined in Section 4.3.21.1.

i). Radial double-wall thickness and lumen width of latewood tracheids : There are pronounced differences between trees in the wall thickness of latewood tracheids at a given height, and the pattern of variation of wall thickness with height is highly variable between trees. The pooled average estimate for all trees shows a low-order linear decrease with height (from 17.11 microns at breast height to 14.03 microns at 60% of tree height).

There are considerable differences between trees in the lumen width of the latewood tracheids. The pooled average estimate increases between 10% (19.93 microns) and 20% (22.37 microns) of tree height, then remains relatively constant to 60% of tree height (22.67 microns). The variation of lumen width with height within individual trees is, in general, less pronounced than the corresponding variation of wall thickness. In general, trees with thick latewood cell walls tend to have narrow cell lumens, and this relationship holds at all heights.

ii). Radial double-wall thickness and lumen width of earlywood tracheids : The pooled average estimate of earlywood tracheid double-wall thickness decreases slightly to 20% of tree height (9.24 microns at breast height; 8.33 microns at 20%) then remains constant to 60% of tree height (8.29 microns at 60%). In most trees the wall thickness remains relatively constant with height; the main differences between trees in the trend occurring in the lower stem. The major aspect of the variation between trees is in the absolute value of this character at a given level..

The pooled average estimate of lumen width of the earlywood tracheids remains almost constant with height; the variation being a negligible portion of the mean value of 49.5 microns. Within individual trees the lumen width tends to remain relatively constant with height. A large component of the between-tree variation is associated with differences in the absolute value of earlywood lumen width at a given height. There is no consistent relationship between trees in the relative values of wall thickness and lumen width of the earlywood tracheids; thick-walled tracheids may be associated with wide or narrow lumens.

iii). Latewood tracheids of the more vigorous trees tend to have wider lumens, and a similar, though weaker, relationship of tree

vigour with earlywood tracheid lumen width exists. No such relationship between tree vigour and wall thickness of either the latewood or earlywood tracheids is evident.

14. The variation with height of the radial double-wall thickness and lumen width of latewood and earlywood tracheids in the oblique series was examined in the third growth layer from the bark (Sections 4.3.21.2. and 4.3.22.).

i). Radial double-wall thickness and lumen width of latewood tracheids: There is a systematic decrease with height (c.f., increase with age) of the pooled estimate of latewood wall thickness : The decrease is most abrupt in the upper crown from 60% to 80% of tree height (19.2 microns at breast height; 14.0 microns at 60%; 9.8 microns at 80%). Within individual trees there is a general decrease in wall thickness with height, but there are considerable differences between trees in the pattern of variation of wall thickness with height. There is a consistent decrease only between 60% and 80% of tree height (i.e., in wood formed in close proximity to or within the living crown). There are considerable differences between trees in wall thickness at a given height (e.g., range 21.2 to 13.9 microns at 20%).

The pooled average estimate of the lumen width of latewood tracheids remains constant to 20% of tree height (18.5 microns) then increases linearly with height (to 23.2 microns at 80%).

There is considerable variability between trees in the pattern of variation of lumen width with height in the lower bole, but between 20% and 80% of tree height there is a pattern of regular increase in most trees. There are considerable differences between trees in the lumen width at a given height (e.g., range 28.5 to 9.8 microns at 20% of tree height).

The radial width of latewood tracheids remains almost constant with height, i.e., it is independent of the age of the cambium forming the tissues.

ii). Radial double-wall thickness and lumen width of earlywood tracheids : There is a systematic decrease in the pooled average estimate of earlywood tracheid wall thickness with height (from 10.3 microns at breast height to 7.6 microns at 80%). There is

considerable variation between trees in the pattern of variation of wall thickness with height : The differences are most pronounced in the lower stem to 20% of tree height (tissues derived from an older cambium well removed from the live crown), and in most trees there is a more or less regular gradual decrease from 20% to 80% of tree height. The variation of wall thickness with height, particularly in the upper stem, is always much more pronounced in the latewood cells. The between-tree range of wall thickness at a given level is a considerable portion of the mean tree value (e.g., 11.7 to 7.0 microns at 20%).

There are considerable differences between trees in the pattern of variation of earlywood tracheid lumen width with height. Within many trees lumen width remains relatively constant to 60% of tree height, and decreases sharply between 60% and 80% of tree height. The pooled average estimate increases from breast height (50.1 microns) to a maximum (53.2 microns) at 20% of tree height, then decreases with height, gradually to 60% (50.3 microns), and abruptly from 60% to 80% (40.7 microns) of tree height. There are considerable between-tree differences in earlywood lumen width at a given height (e.g., 66.9 to 43.2 microns at 20% of tree height).

There is a quadratic trend of variation of earlywood cell width with height, generally similar to that of lumen diameter; i.e., with increasing height earlywood cell width increases (from 60.4 microns at breast height) to a maximum value (62.3 microns) at 20% of tree height, and then decreases (58.6 microns at 60%; 48.3 microns at 80%).

15. The variation of radial cross-sectional dimensions of latewood and earlywood tracheids outward from the pith in selected growth rings at six height levels was examined in Section 4.3.22. Because of the sampling intensity, the pattern of variation of anatomical characteristics with age is more comprehensively described in the oblique series (as with height within the third growth sheath from bark - 14. above).

i). Radial double-wall thickness and lumen diameter of latewood tracheids : There is a pronounced systematic increase in the wall thickness of latewood tracheids outward from the pith at each height level : The rate of increase is rapid initially but declines with

increasing age. Latewood tracheid lumen width decreases outward from the pith : The rate of decrease is rapid over the inner rings but declines with increasing age. Latewood cell width decreases outwards from the pith over the innermost growth rings then remains relatively constant.

ii). Radial double-wall thickness and lumen width of earlywood tracheids : There is a systematic increase of wall thickness of the earlywood tracheids outward from the pith at each height level. The variation of wall thickness with age is more pronounced in the latewood than in the earlywood cells. The lumen width of earlywood tracheids is lowest in the innermost rings, and remains relatively stable with increasing age from the pith. There is a general low-order increase in earlywood cell width outward from the pith. N.B. The consistent low-order quadratic trend of variation (increase with height to a maximum value then decrease) of both lumen and cell width with age, demonstrated in the oblique series (see 15.), may be obscured in the horizontal series by the low sampling intensity. Radial wall thickness does not appear to have reached a maximum value in the material of this study.

16. The variation of earlywood tracheid length within the stem was examined in Section 4.3.3. Tracheid length increases outward from the pith at each height level. Within an annual growth sheath there is a quadratic trend of variation of tracheid length with height : Tracheid length increases with height to a maximum value, which occurs in the lower stem well below the region of the living crown, and then decreases progressively towards the stem apex.

There is little variation in the arithmetic disc average value of tracheid length with height in the stem (whole-tree arithmetic mean 4.751mm). There is a considerable range of between-tree variation of tracheid length.

17. The effect upon the estimate of whole-tree values of wood characters of the height in the stem at which a wood sample is taken was examined in Section 4.4. The degree to which the value of a wood character estimated from measures of a pith-to-bark sample at various height levels (breast height, 10%, 20%, 40%, 60%, and 80% of tree height) is representative of the whole-tree value

was examined by correlation analysis. Linear regression analysis was used to indicate the accuracy of prediction of whole-tree values from the values derived from measures taken at different levels.

i). For each of the densitometric characters (ring maximum, minimum, and mean density; density range; latewood percentage) the correlation of the values (derived both as arithmetic and weighted estimates) from each of the discs to 60% of tree height with the whole-tree estimate is highly significant, indicating that estimates derived from a pith-to-bark sample taken at any given level between breast height and 60% of total tree height may be taken to represent faithfully the whole-tree value for the purpose of between-tree comparison. For each of these characters other than minimum density, the correlation of the whole-tree value with the disc value at 80% of tree height is also high. For each of the densitometric characters discs taken below 60% of tree height (from breast height to 40%) yield estimates more closely representative of whole-tree values.

ii). There are substantial phenotypic differences between trees in the weighted whole-tree average values of ring maximum density : range 0.618 to 0.961 or 43% of the mean value (0.798). The sample error associated with the prediction of the whole-tree value from disc values at various height levels is very low; e.g., the standard error of estimate of the regression of the weighted whole-tree values on the disc values at 20% of tree height is 0.007, or less than 1% of the mean.

iii).The range of estimate of whole-tree mean density between trees (0.414 to 0.594) is high (36%) in relation to the mean tree value (0.495) : the sample error (less than 1% of the mean value at 20% of tree height) is again low.

iv). The range of values between trees for the weighted whole-tree intraincremental density range is from 0.303 to 0.601 or 66% of the mean whole-tree value (0.450), while the sample error (0.007) at 20% of tree height is less than 2% of the mean.

v). There are very large phenotypic differences between trees in the weighted whole-tree average values of latewood percentage : values range from 17.28% to 64.32% or 128% of the mean whole-tree value (36.81%). The sample error at 20% of tree height (0.777)

is negligible.

vi). For each of the densitometric characters the disc average estimate at 20% of tree height very closely approximates the whole-tree average value. Average values of each character estimated from measures of discs taken below and above 20% of tree height overestimate and underestimate respectively the whole-tree average value of the character.

vii).For each of the tracheid radial cross-sectional dimensions, (double-wall thickness, lumen width, and cell width in each of the intraincremental earlywood and latewood zones) the correlation of each of the disc arithmetic average values (from breast height to 60%) with the whole-tree arithmetic average values is highly significant, indicating that estimates derived from a pith-to-bark sample taken at any given level between breast height and 60% of total tree height may be taken to represent faithfully the whole-tree value in between-tree comparison.

viii).There is a high degree of phenotypic variation between trees with each of the tracheid cross-sectional dimensions. In each case the sample error is very small in relation to the between-tree differences, and the regression equations of whole-tree values on disc values are highly significant.

ix). The phenotypic differences between trees are considerably less for tracheid length than for tracheid C.S. dimensions. Arithmetic whole-tree average values range from 4.240 to 4.847mm or 13% of the mean whole-tree value (4.571mm). Sample error ranges from 0.6% of the mean value (at breast height) to 1.5% (at 20% of tree height). The regression of whole-tree values on disc values is highly significant at breast height but not significant at 20% of tree height. Estimates of tracheid length derived from a pith-to-bark sample taken from breast height faithfully represent the whole-tree value, but estimates derived from a sample at 20% of tree height are not representative of whole-tree values and are unsuitable for between-tree comparison.

18. In Section 4.5. an estimate was made of the effects upon the variation of the wood characteristics (13 'response' characters :

6 wood density variables; 7 cell dimensions) of radial growth rate and of position associated with height in the stem and with age and radial distance from the pith (5 'stimulus' characters : ring width; age of growth ring; radial distance from pith; percentage of total tree height; height in stem).

i). The intercorrelation of individual 'stimulus' and 'response' characters was examined : There is a high level of significant intercorrelation of stimulus and response variables (54 and 43 of the 65 coefficients are significant at the 5% and 1% level respectively). The coefficients are consistently high for correlations between each of the stimulus characters and the densitometric characters , tracheid length, and latewood tracheid wall thickness.

The combined stimulus variables account for a considerable portion (roughly 50%) of the variation of each of the densitometric variables. Of the tracheid dimensions, the variation of tracheid length is most faithfully predicted (R^2 = 0.71) by the combined measures of height, radial position, and growth rate; between 31% and 45% of the variance of the latewood C.S. dimensions are accounted for, but the earlywood tracheid C.S. dimensions are each poorly predicted.

ii). The matrix of intercorrelations among the 13 'response' characters was resolved and reduced to relative simplicity (summarised) using principal components analysis : The orthogonal linear combinations of variables are generally similar to those interpreted in Section 4.2. (see 7. of Summary).

Coefficients of correlation between the principal components of the response characters and the individual stimulus characters are presented. The moderately high values of R (0.76 - 0.56) for the multiple regressions of each of the first 3 response components on the stimulus variables suggest that appropriate functions of the stimulus characters (height, radial position, and growth rate) would have some value in predicting meaningful combinations of response characters.

iii). Simple correlation analysis proved ineffective in evaluating the relative influence of radial growth and position effects upon the development of wood characters, because the pronounced systematic

variation within individual stems of many of the wood characters and ring width is approximately collinear with that of ring age. The statistical interdependence (collinearity) of the several stimulus variables and the response variables has proved an obstacle to the quantative evaluation of the relative importance of radial position effects (ring age, distance from pith) and ring width, and has resulted in many examples in the literature of misinterpretation and confusion of the effect of age with the effect of growth rate.

iv). Principal components analysis of the 'stimulus' character complex was used to derive orthogonal vectors representing height and radial position and growth rate. The first component, w_1, is a vector representing height, and is almost completely correlated ($r = 0.99$) with each of the height measures. w_2 is a vector of radial position very strongly associated with ring age ($r = +0.93$) and strongly (+0.73) with ring distance from the pith. The third component, w_3, is a vector representing growth rate that is independent of ring age ($r = 0.03$) and height (-0.09, 0.01).

The 3 components effectively account for 100% of the variance of the standardised stimulus variables. Note : The principal components of the stimulus characters, which represent height, age and distance of the growth ring from the pith, and radial growth rate, respectively, are (in contrast to the individual stimulus variables) statistically independent of one another (orthogonal). As a consequence, indices of affinity (correlation coefficients) between the stimulus components and the response variables or components provide appropriate estimates of the relative importance of the relationship of each stimulus component with the response characters or character combinations.

v). The first response component, z_1, is strongly correlated with the first (height effect), and second (ring age and distance from the pith) stimulus components, but has no affinity with the third stimulus component (growth rate). N.B., z_1 is a vector representing the densitometric characters (maximum density ($r = 0.93$), mean density (0.90), density range (0.87) and latewood percentage (0.83)) and the contrast of wall thickness (0.83) and lumen width (-0.74) of the latewood tracheids. Thus, the variation of the densitometric characters and the closely associated variation of lumen width and

wall thickness of the latewood tracheids is independent of radial growth rate *per se* , but is strongly associated with radial and axial position within individual trees. The simple correlations of these response characters with ring width was a result of co-response to a common factor, i.e., to position effects.

The second response component, z_2, shows negligible correlation with either the first (height effect) or second (ring age and distance from pith) stimulus component, but is strongly correlated with the third stimulus component (radial growth rate). N.B., z_2 is a vector representing the variation of lumen width ($r = 0.88$) and overall C.S. size (0.86) of earlywood tracheids and the associated minimum (earlywood) density (-0.48), but independent (in a statistical sense) of earlywood tracheid wall thickness. Thus, the lumen and cell widths of the earlywood tracheids and associated low density of the earlywood are not affected by position within the stem, but are strongly influenced by radial growth rate.

The third response component, z_3, is most strongly correlated with the third stimulus component (radial growth rate). z_3 is a vector closely associated with the radial width of the intraincremental latewood zone and with the overall C.S. dimensions of the latewood cells. Thus, the width of the intraincremental latewood zone and the associated cell width of the latewood tracheids are strongly influenced by radial growth rate.

19. Some features of the growth and morphology of the trees and their relationship with the wood characteristics were examined in Section 4.6.

i). Stem analyses were made, and the patterns of growth of the individual trees are depicted graphically (periodic and mean volume increments; height:age curves; taper curves). The patterns of development show :

a). The relative vigour (dominance status) of the trees is established at an early age (less than 10 years) and remains essentially similar with age.

b). The annual volume increment has reached a maximum value and begun to decline progressively in the most strongly suppressed trees.

c). The growth response of the trees shows no evidence of increase in ecophysiological stress as the stand ages.

ii). The intercorrelation of 7 morphological features (tree height; height to base of the green crown; length of the green crown; stem diameter (u.b.) at breast height; height/d.b.h. (taper); stem taper; total stem volume (u.b.)) was examined. Tree volume is very strongly correlated with height, d.b.h., and each of the two estimates of stem taper, and there is a high degree of intercorrelation among these variables.

iii). The whole-tree wood mean density (weighted estimate) is most strongly associated with stem taper. There is a significant negative correlation between whole-tree mean density and the breast height diameter and total volume of the trees. Notable exceptions to this general tendency are apparent : Codominants of comparable vigour may produce wood of relatively high or of low density. There is very considerable between-tree variation in the intraincremental density contrast (wood texture) among trees of comparably high vigour. Whole-tree density is unrelated (statistically) to tree height or to the length of the living crown.

20. The nutritional status of the soil and the foliage was examined (Section 4.7.). Measures of total levels of 9 chemical elements (N, P, Ca, K, Mg, Na, Fe, Mn, Zn) in both topsoil and foliage, and of pH and % loss on ignition in topsoil, were examined (see Appendix 2 for analytical techniques).

The interrelationships between individual nutrient factors and complexes of interrelated factors in the soil and in the foliage were identified and estimated by principal components analyses of the standardised measures.

i). Topsoil : There is a high degree of variation between samples for all the elements. Values for total phosphorus are very low (undetected at 65% of sample locations). There is a moderate degree of intercorrelation among the soil characters : 11 of the 55 coefficients are significant at the 5% level. Complexes of soil characters (characters which tend to co-occur in highest and lowest concentration) were identified on the first 4 principal components of the standardised soil character measures : %LI, Fe, N, Mg, K (component 1); contrast of (P, Ca) and (Zn, Mn) (component 2);

contrast of Ca and Na (component 3); pH, Mn (component 4).

ii). Foliage: There is considerable variation between trees for each element. Between sample variation is of a lower order than that of corresponding elements in the soil samples for all elements other than K, the level of which is more variable in the foliage. Foliage P levels are generally low (mean 0.066%; range 0.049% to 0.096%). The extent of intercorrelation among the foliage nutrients is low (4 of 36 coefficients significant at the 5% level). Complexes of nutrients (which tend to co-occur in greatest and least abundance) were identified on the first 3 principal components : contrast of (Mg, Ca, Mn) and (Fe, P) (component 1); contrast of (N, Zn, P) and (K) (component 2); P, K, Na, Ca (component 3).

21. Relationships between the level of nutrients in the topsoil and foliage were examined (Section 4.7.c). The overall affinity of the nutrient levels of the soil and foliage is low. Only 2 of the 9 foliage elements, Ca and K, are significantly correlated with nutrient factors in the soil. Both are positively correlated with soil pH. 81% and 57% of the variation of foliage K and Ca respectively are accounted for by the combined soil measures.

The interrelationships between the foliage nutrient complexes and the soil factors and factor-complexes are, in general, relatively weak and difficult to interpret in terms of the effects of the measured soil features on the nutrient status of the foliage. The levels of specific elements in the foliage often bear little relation, or a negative relation (e.g.,K) to the total level of these elements in the soil. Soil pH is related to the second and third foliage components which represent, respectively, the contrast of (N, Zn, P) and (K), and a positively associated complex of (P, K, Na, Ca).

22. The between-tree source of random variation of 12 wood characters (weighted whole-tree estimates of 6 densitometric characters, and arithmetic whole-tree estimates of 6 cell dimensions) was examined (Section 4.7.d). There is a high degree of intercorrelation among the wood characters. Each of the wood characters has its highest loading on either of the first 2 principal components, which together

account for almost 80% of the variance of the standardised whole-tree estimates of all characters.

The first component, z_1, is most highly correlated with wood mean density (r = 0.96) and latewood percentage (0.93). It is characterised by the close positive affinity of the densitometric characters and the strong correlation with the contrast between the wall thickness and (lumen and cell width) of the latewood tracheids. Thus, the values of the wood characters in the complex (mean, maximum and minimum density; latewood percentage; density range; and latewood tracheid wall thickness) tend to be simultaneously high in trees in which the lumen and cell widths of the latewood tracheids is low (and vice versa).

The second component, z_2, is an orthogonal linear combination of variables most strongly representing variation in the C.S. dimensions of the earlywood tracheids. There is a close positive association of wall thickness, lumen and cell widths of the earlywood tracheids, and the width of the intraincremental latewood zone.

The third component, z_3, represents variation of earlywood tracheid wall thickness and minimum (earlywood) density.

23. The interrelationships between the wood characteristics of the trees and the nutritional features of the foliage and soil were examined (Section 4.7.e. and f.).

i). There is a moderately strong relationship between the foliage nutrient levels and the lumen and cell widths of the tracheids; the strongest relationships involving these anatomical characteristics of the earlywood cells. The relationships effectively involve only 3 (N, K, Fe) of the 9 foliage elements examined. The tracheid lumen and cell widths in the earlywood show a close positive association with foliar Ca and K levels. Ca is positively associated with earlywood tracheid wall thickness also. The level of Fe in the foliage is strongly associated with the lumen and cell widths of the latewood tracheids. Foliage K has a moderate positive affinity with these latewood anatomical traits. The relationships of the foliar elements with wall thickness of the latewood tracheids are, in contrast, weak or

negligible.

Of the densitometric characters, minimum (earlywood) density shows some relation to the overall nutrient status of the foliage and is negatively related to the level of Zn in the foliage, and the width of the intraincremental latewood zone is positively associated with the level of foliage Fe; but the relationships of the other densitometric characters with the foliage nutrients are poorly defined.

Over 50% (R^2 x 100) of the variation of each of 7 of the 12 wood characters is accounted for by the combined measures of the foliage elements. The coefficient of determination, R^2, is highest for the lumen and cell widths of both earlywood (0.67, 0.69) and latewood (0.59, 0.64) tracheids and minimum (earlywood) density (0.69); i.e., roughly 60% to 70% of the variation between trees in these wood characters is predicted by the combined foliage nutrient measures.

The first principal component of the wood characters (a vector representing the variation of the densitometric characters (mean, maximum and minimum density; latewood percentage; density range) and the contrast of lumen and cell widths and the wall thickness of latewood tracheids) has a weak to negligible affinity with each of the foliage elements and element complexes (components).

The second principal component of the wood characters (a vector strongly representing the variation of C.S. dimensions of earlywood tracheids) shows some affinity with each of the foliage elements Fe, Ca, and Na, and with the foliage nutrient complex (P, K, Na, Ca - third foliage component).

The third wood character component (earlywood tracheid wall thickness and minimum (earlywood) density) is related to each of the foliage elements Ca, Zn, K, and Mn and the first 2 foliage nutrient components. The relationships, although consistent, are relatively weak.

ii). The relationships between the measured soil features and the wood characteristics of the trees are generally negligible or weak and poorly defined. There is some relationship between the anatomical charasteristics of the earlywood tracheids and the measured soil features; a relationship most consistently associated

with soil pH, which has a moderately strong positive affinity with the wall and lumen dimensions of the earlywood tracheids.

24. Data showing the magnitude and patterns of variation of a series of wood characters in trees of age and provenance comparable with those of the Beerburrum study, growing in plots on 3 sites of diverse ecology in tropical North Queensland are presented in an annex to the thesis (Appendix 3). The data are extracted from the results of an independent study. They indicate the extraordinarily broad spectrum of response of wood characteristics in var.hondurensis to the influence of variable site factors. Some noteable features of this variability are :

i). A major aspect of the variation between plots is associated with the patterns of development in the stem and the magnitude of the intraincremental density contrast (texture) : features determined by the variation of ring maximum (latewood) density.

ii). Interrelationships among the densitometric characters are essentially similar in the wood from each of the northern plots and the Beerburrum material.

iii). As was the case with the Beerburrum material, measures of pith-to-bark samples taken at any given level from breast height to 60% of tree height provide estimates of the densitometric characters that are representative of whole-tree values and thus facilitate valid between-tree comparison.

The data presented in Appendix 3 are alluded to in comparative discussion in Chapter 5.

CHAPTER 1

INTRODUCTION

The establishment of new forests of exotic conifers in tropical and subtropical countries has attracted increasing interest in the past decade. Development of forest resources is an important activity in developing countries: It assumes increasing urgency to avoid or to alleviate shortages of forest products, often critical, and to create economic stimulus and stability in an environment of rapidly increasing population and socio-economic change.

Much of the impetus that has encouraged programmes of afforestation by exotic conifers in the tropics arose from the pioneer studies of Caribbean pine by Luckhoff [Luckhoff, 1964] which provided a comprehensive account of the growth of *Pinus caribaea* in its native habitat and in plantations established in subtropical regions of South Africa. This early work, and subsequent studies, indicate the potential of the species for rapid growth on seasonally arid and infertile sites at low altitude in the tropics. In the lowland tropics there exist vast areas of depauperate land, often impoverished through exploitation and adverse cultural practices, but potentially suited to the growth of this species. Restoration of forest cover on these areas, which are at present unproductive and often exposed to continued degeneration as a result of burning, leaching, and surface erosion, could provide lasting benefit through stabilisation and wood production. *Pinus caribaea* has become the most important species of timber tree being planted in the lowland tropics, and programmes of artificial reforestation are increasing in number and scale.

High stem volume production has been reported for plantings of Caribbean pine as an exotic in subtropical regions of Natal province, South Africa [Luckhoff, 1964; de Villiers, 1973] and southern coastal Queensland [Nikles, Hawkins, Simpson, 1971; Smith, 1973]. But despite the potential of the species for increased volume yield, plantings have

virtually ceased in South Africa because of undesirable timber properties associated with wood of low density. In southeastern Queensland plantings of Caribbean pine continue on a modest scale: The potential of the species for increasing production is only marginally realised largely because of uncertainties of its wood qualities, and because of current inadequate availability of high quality seed and the need for a relatively expensive establishment technique using tubed stock. There is a critical need for detailed research to resolve uncertainties regarding wood properties, particularly those properties that have become, or are expected to become, of importance in processing or in the suitability of the manufactured products for various end uses. Yet, because of its rapid growth, Pinus caribaea remain a potentially valuable species for exotic afforestation in subtropical areas as a means to increased production and reduction of crop rotation intervals.

1.1 CARIBBEAN PINE

The pines of Central America and the Caribbean islands form the southernmost extension of the genus *Pinus* in the New World. The Caribbean pine, *Pinus caribaea* Morelet , forms three geographic varieties: var. *caribaea* Barr.and Golf.,which is confined to western Cuba at altitudes ranging from 50 to 300 metres; var. *bahamensis* Barr. and Golf., which occurs in the Bahamas and Caicos Islands at low elevation; and var. *hondurensis*.* The latter, var. *hondurensis*, occurs naturally on the Central American mainland at altitudes ranging from sea level to 850 metres, and from about 12°13' N in Nicaragua to almost the northern border of British Honduras, at 18° N. The taxonomy of the species has been revised by Barrett and Golfari [1962] and is discussed in detail by Luckhoff [1964] and by Lamb [1973]. Comprehensive accounts of the growth and behaviour of *P. caribaea* in its native habitat are presented by Luckhoff [1964], Nikles [1966], Lamb [1973], and Kemp [1973].

The recent upsurge of interest in the species as a commercial crop has resulted in a very extensive programme of provenance trials, particularly of var. *hondurensis*, in many tropical and subtropical

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* To avoid excessive repetition, each variety will be referred to in the text by the varietal name only.

countries. Plantation on a commercial scale is under way, notably in Fiji, Queensland, Brazil, Jamaica, and Tanzania: var. hondurensis is now the most extensively planted timber tree of the lowland tropics. A great deal of information about the exotic afforestation of *Pinus caribaea* has been compiled in a recently published monograph [Lamb, 1973].

P. caribaea var. *hondurensis* was introduced to Queensland in 1948. Approximately 4500 ha. of plantation was established by 1973, mainly on coastal lowlands between 17° S and 27° S from seed collected in the Mountain Pine Ridge region of British Honduras (approximately 2000 ha.), and, since 1961, from local select seed [Hawkins, Nikles, Smith, 1972; Nikles, 1973b]. The annual planting rate in 1973 was 400 ha. Early growth of var. *hondurensis* is superior to that of *Pinus elliottii* var. *elliottii*, the most extensively planted exotic, on all sites that are freely drained and not subject to severe frosts. An extensive programme of provenance trials has been undertaken since 1956 [Nikles, 1973a,b].

1.2 THE WOOD: STRUCTURAL FEATURES AND PROPERTIES

The wood of var. *hondurensis* from natural forests is known as yellow or pitch pine: It is suited to a general range of uses including light and heavy construction, piles and sleepers, particle boards, and furniture making [Hughes, 1967; Lamb, 1973], and has a long history of exports from Honduras to the U.S.A. and Britain. The timber from natural forests is regarded as heavier and stronger than that of *Pinus elliottii* and *Pinus palustris* from the United States; but a central core of light wood is commonly found and must be eliminated from structural grades.

A very substantial degree of variation of wood structure and properties in different trees from natural forests has been demonstrated [Hughes, 1970; Lantican, 1971]. Aspects of cyclic growth behaviour, and many of the wood characteristics appear to exhibit considerable genotypic variation and to vary quite markedly in response to different environmental conditions.

A range of habitats more diverse than that found in the natural range is encountered in the extensive exotic afforestation of var. *hondurensis* in the tropics and subtropics. Pronounced interaction of a genetic/environmental nature is encountered in the introduction of

provenances to site conditions to which they are not inherently adapted. The effects are manifest as a wide range of variability of stem form and growth [see Kozlowski, Greathouse, 1970; Nikles, 1973b; Lamb, 1973] and of wood features [see Burley, Nikles, 1973b]. As a consequence, a knowledge of the wood structure and properties of the species grown in its native habitat does not provide an adequate basis upon which to predict the quality of the wood it will produce in an exotic environment.

Although var. *hondurensis* is widely and increasingly used for afforestation in many parts of the world, the quality of the wood produced has, in general, received relatively superficial evaluation: In particular, little is known about the patterns of variation of many structural features and properties of the wood that are important to an assessment of wood quality in the species. Much of the recent knowledge of wood features of var. *hondurensis* is summarised in two recent publications [Burley, Nikles, 1973b; Lamb, 1973].

Reports of wood properties and structural features indicate that a considerable degree of variation can be encountered. Concern has been expressed for the high incidence of compression wood found in young stems [Hughes, 1967; Boone, Chudnoff, 1972] which may cause degrade in seasoning and reduced yield and strength in pulping. Large central zones of low density wood are commonly found. This feature of structural development, which is commonly encountered in tropical plantation-grown species [see Hughes, 1968; Hardie, Ingram, 1973; de Villiers, 1973], may present difficult problems in conversion and use of material intended for sawlogs. Degrade resulting from massive resin impregnation is reported from trees over 15 years of age grown in subtropical regions of South Africa [Luckhoff, 1964; de Villiers, 1973].

Considerable variation in pulping and papermaking characteristics of the wood of young trees from a number of different countries has been reported [Chittenden, Jarman, Palmer, Hughes, 1967; Palmer, Peh, 1966; Palmer, Tabb, 1968, 1973; Watson, Higgins, Smith, 1971; Palmer, Gibbs, 1972]. Pulp from trees growing under favourable conditions has strength properties similar to those of a commercial grade Southern pine sulphate pulp, and papermaking qualities are satisfactory. Preliminary tests indicate the suitability of the wood of plantation-grown var. *hondurensis* for commercial production of particleboard [Packman, 1959; Chittenden, Flaws, Hamilton, Hawkes, 1972].

In Queensland *Pinus caribaea* is regarded as a potentially valuable general purpose softwood species, giving high yields over a very wide range of ecological conditions [Smith, 1973; van Altena, 1973]. The available information on recoverable yields, properties and quality of the wood of var. *hondurensis* grown in Queensland is largely summarised in a recent publication [Smith, 1973]. There is a compelling need for further information on the structural features and properties of the wood produced. The potential of the species for increasing volume yield over a wide range of ecological situations in Queensland has been demonstrated, and a comprehensive programme of improvement through selection and breeding has resulted in real gains, particularly in stem straightness and crown form [Slee, Nikles, 1968; Nikles, 1973b] and indicated potential for further genetic improvement. But a very much more detailed and comprehensive knowledge of the wood quality is a critical prerequisite of commitment to a major planting scheme.

Little is known of the patterns of variation of wood density features within trees grown in Queensland plantations. The effects upon wood quality of pronounced within-tree variation of structural features may be of much greater practical importance than differences in mean values between trees. The limited estimates of population parameters that are available have been derived from samples taken from a single level in the lower stem of individual trees: The relationships between the values of structural features derived from these measures and the corresponding whole-tree values are not known.

Of the anatomical characteristic of the wood, tracheid length alone has been studied in any detail: Within-tree patterns of variation have not been defined. The variation of wall thickness, lumen and cell widths of the tracheids is unknown: Yet these anatomical characteristics are known to affect such wood properties as strength, shrinkage and swelling, permeability, gluing and pulping and machining characteristics [Goggans, 1965; Orman, Harris, 1965; van Buijtenen, 1969]. In the technology of pulp and paper making, there is increasing evidence that tracheid cross-sectional dimensions influence paper properties to a greater extent than does tracheid length [Dinwoodie, 1965; van Buijtenen, 1969; Panshin, de Zeeuw, 1970]. The study of variation of tracheid

cross-sectional dimensions is an area of research, the importance of which is widely recognised, but which has suffered general neglect [see Tappi, 1960; Goggans, 1965; Orman, Harris, 1965; Shultz-Dewitz, 1965].

The present study was undertaken with a view to evaluating and assessing the variation of some structural features of the wood of var. *hondurensis* grown in Queensland. The trees to be studied were selected from some of the oldest exotic plantings of var. *hondurensis* outside of South Africa. Several structural features were chosen that are known to exert an important influence upon the industrial processing of the wood and upon the suitability of the manufactured products for various end uses.

Wood density* is the most widely used index of wood quality. It can be measured precisely with relative ease, and is correlated strongly with many wood characteristics of commercial importance. In this study the technique of X-ray densitometry is used to measure a profile of wood density features. Wood density is a compound character, integrating the variation of a complex of anatomical attributes of which the wall thickness, lumen and cell diameter and cell length of the tracheids are of particular significance. The variation of each of these anatomical characters is examined. They are each known to exert a specific influence upon properties of the wood that are important to utilisation. A knowledge of their variation is fundamental to an understanding of the processes controlling variation in wood density; particularly since the wall and cell diameter of tracheids are known to be controlled ultimately by independent physiological processes.

1.3 A SUMMARY OF THE AIMS OF THIS STUDY

The main objectives of the research effort reported in this thesis are:

(i) To evaluate and to assess the extent and patterns of variation of selected wood characters within and between trees from one of the oldest established routine plantings of var. *hondurensis* in southern coastal Queensland.

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* Wood density and specific gravity are equivalent in the metric system. The term wood density is used throughout the text.

(ii) To determine the relationships between estimates of the values of wood characters derived from measures of small-scale samples and the corresponding whole-tree estimates of these features.

(iii) To examine the inter-relationships among the wood characters.

(iv) To ascertain the extent to which the variation of the wood characters is associated with age and position within the stem, rate of growth, and other morphological attributes, and to estimate the effects upon wood characteristics of growth rate and position within the stem; and

(v) To examine some nutritional features of the soil and foliage and to assess their inter-relationship with wood characteristics of the trees.

A range of analytical techniques is used in pursuit of these objectives. Some of the analytical approaches adopted in this study, and in particular techniques of analysis of inter-relationships among large numbers of variables, are used in combinations that have seldom, if ever, been applied to problems of a similar nature in wood quality studies.

The content of this thesis summarises the results of an integral portion of a much larger programme of research of the variation of wood characteristics of Queensland-grown var. *hondurensis* undertaken by the author. This initial study involves the detailed analysis of the wood features of twenty trees selected from a routine planting established in 1953 at Beerburrum forest in southern coastal Queensland (latitude 27° S). The research programme included a similarly detailed analysis of the wood features of trees of a similar age to those reported in this study grown in each of three trial plots at widely varying altitude in tropical north Queensland (17° S) and in three further trial plots of variable site index in the State forests at Toolara and Tuan (26° S) in southern Queensland. The data of this research has been acquired and analysed: Some of these results are alluded to in general discussion; but their detailed presentation is beyond the scope of this thesis, and the results of this extended research effort will be published independently at a future date.

1.4 SOME CONVENTIONS USED IN THE PRESENTATION OF THE TEXT

The following conventions have been adopted to effect clarity and concision in the presentation of the text:

(i) Values for wood density are calculated as g/cm^3: But the units are not quoted in the text.

(ii) In the tabular presentation of coefficients of correlation and of eigenvector elements the decimal point is omitted.

(iii) Statistical significance at the 5%, 1% and 0.1% levels is denoted by *, **, and ***, respectively, in the tabular presentation of analyses of variance and of coefficients of correlation.

CHAPTER 2

THE ACQUISITION OF MATERIAL IN THE FIELD: TECHNIQUES OF SAMPLING

2.1 THE SELECTION OF TREES WITHIN A STAND

The most important feature of a sample is that it is representative of the population from which it is drawn. This may be achieved by random selection of the sample elements: But the efficiency of sampling may be increased by prior stratification of the population in relation to the character under study or to some more readily identified feature related to it. Visual selection on the basis of wood characteristics is not possible, and stem diameter at breast height (1.3 m), is commonly used to stratify a population of trees to facilitate the selection of sample elements (trees) for the study of wood characteristics [see, e.g., Wolski, 1968].

The method of ranked-set sampling developed by McIntyre [1952] can effectively provide an unbiased sample of minimum size, and its application in the field situation is rapid and equivalent in simplicity to subjective methods of selection. Ranked-set sampling has been used effectively to estimate forage yields [McIntyre, 1952; Halls, Dell, 1966], and wood density features in stands of *Pinus radiata* [McKinnell, 1970].

The procedure of ranked-set sampling may be summarised as follows: Within a set of n random items, the largest with respect to the characteristic being sampled is chosen in the first set, the second largest in the second set, and so on to the smallest in the nth set. In practice, individual groups of n trees (where n is the predetermined set size), from each of which one sample tree is drawn, are referred to as sets. Sets are located adjacent to one another, with care being taken not to include individual trees in more than one set. Clusters of n sets are termed plots. The d.b.h. of each of the n trees in each set is measured: The largest tree is drawn from the first set, the second

largest from the second set, and so on to the smallest tree in the nth set; to yield a plot sample of n trees.

Special features of Ranked-set sampling are:

(i) The n items are an unbiased sample of the population. Thus, for a set of reasonable size, say 10, the frequency distribution of diameters in the set will approximate that of the stand.

(ii) Where there are no errors in ranking and the frequency distribution of the characteristic being measured is symmetrical, the efficiency of estimation of the mean, relative to random sampling, is about $\left(\frac{n+1}{2}\right)$; i.e., for sets of 10, $\left(\frac{10+1}{2}\right)$ or 550%.

(iii) The technique is particularly suited to the situation where the local variation (such as d.b.h., or wood density, between trees) is greater than the variation between set areas (average d.b.h., or wood density) from one part of a stand to another .

A high degree of accuracy in ranking on d.b.h. can be achieved: But the precision of the method with respect to the estimates of wood character values cannot be inferred from this; although whole-tree wood density is significantly correlated with the attributes of vigour (Section 4.6).

2.2 SELECTION AND EXTRACTION OF SAMPLE MATERIAL FROM INDIVIDUAL TREES

(a) Wood Samples

The system used to locate wood samples within individual trees should be designed to yield data suitable for valid between-tree comparison of wood properties. Numerous studies of wood characteristics of a wide range of coniferous species have indicated marked systematic variation within individual stems. Much of this variation is associated with the age of the cambium at the time the wood was formed. The implications of systematic variation for sampling of wood characteristics has received considerable attention in the literature [e.g., Duff, Nolan, 1953; Richardson, 1961; Balodis, 1966].

A sample reference system using ring number from pith and annual height increment from ground level as co-ordinates enables the determination of patterns of systematic variation within stems and facilitates valid between-tree comparison. Co-ordinates assigned to a

specific growth ring and annual height increment remain constant throughout the life of a tree and are independent of the age of the tree, and secondary co-ordinate systems can be derived by the application of simple algebra [Balodis, 1966].

Delimitation of the annual height increment of trees of var. *hondurensis* by examination of branch whorl patterns is very difficult since the trees exhibit multinodal growth [Kozlowski, Greathouse, 1970; Slee, 1972], and there is no conspicuous evidence of a constant pattern of variation of branch diameter within or between annual sets of whorls in most trees. The problem of accurate delimitation of the annual height increment in the lower stem is aggravated by dead branches having been dislodged or removed by pruning.

Since it is not possible to delimit accurately annual height increment, samples were located at levels proportional to the height of the tree. This system is not precisely related to biological variation with respect to time, but it provides an effective compromise [Chalk, 1961; Richardson, 1961].

Trees were felled and discs 6 to 8 cm thick removed from breast height (1.3 m) and from 10%, 20%, 40%, 60% and 80% of total tree height.

The average diameter of each disc was measured with a tape both over bark, and, following debarking, under bark.

Discs were soaked for several hours in 4% formaldehyde solution to minimise the incidence of fungal infestation, and then sealed in polythene bags for transit to the laboratory.

(b) Foliage Samples

Careful standardisation of sampling procedures is essential in the analysis of plant material. Factors which may affect the level of foliage nutrients within the crown include the age of the tissue, the position within the crown, the season, shading, and the incidence of drought or rain prior to sampling. For a given nutrient supply, the physiological age of the tissue is probably the most important factor affecting its mineral composition [Smith, 1962]. To ensure uniformity of

this factor when sampling coniferous foliage, it is generally agreed [Leyton, 1958] that the current season's needles should be sampled, and that the sample should be taken from a specified location within the crown (although there is no agreement as to the most satisfactory position).

A sub-sample of the more fully extended leaves, generally in the penultimate growth whorl of the branch, was removed from each of the branches of the second branch whorl from the stem apex. The sub-samples were mixed to form a composite sample unit of approximately 50 fascicles, and each unit was sealed in a polythene bag for transit to the laboratory.

2.3 THE SELECTION AND SAMPLING OF ENVIRONMENTAL FEATURES

The primary constraint on the choice of habitat features for sampling and analysis was the time available for the collection of samples: This precluded the detailed measure of features that demand extended labour or sampling at repetitive intervals in the field. It was necessary to select, on *a priori* grounds, factors, amenable to quantitative measure, which could have a bearing on the growth and wood properties of trees within the stands, and which might thus provide appropriate indices to characterise the plots. Within the range of factors recorded, the covariation of habitat features with tree growth and wood characteristics can be objectively resolved.

The mineral status of the topsoil was selected for detailed assessment. Little is known of the mineral nutrition of the species, and no published evidence is available of relationships between mineral nutrition and wood characteristics of var. *hondurensis*. But considerable growth response to fertiliser application has been recorded [e.g., Dick, 1969; Platterborze, 1970; Anon., 1965-66, 1968-69; Gardner, 1971, van Altena, 1971], and specific mineral deficiencies have been implicated in the study of growth abnormalities [e.g., Proctor, 1967; Waring, 1971].

This essentially exploratory study of nutritional characteristics of the soil is complemented by an investigation of nutrient levels in the foliage.

Topsoil Samples

Vertical soil cores from the top 10 cm of mineralised soil (below the litter layers) were extracted at four randomly selected positions within 1 m of the stem of each of the trees sampled for the study of wood properties. The four cores were mixed to form a composite sample unit of approximately 800 cc from around the base of each tree. Each unit was sealed in a polythene bag for transit to the laboratory.

CHAPTER 3

LABORATORY ANALYSES OF WOOD SAMPLES

3.1 THE QUANTITATIVE MEASURE OF SOME WOOD FEATURES BY X-RAY DENSITOMETRY

Radiological techniques have, in recent years, facilitated the study of the variation of wood density in much greater detail than was possible using gravimetric techniques. Measurement of density variation is sufficiently precise to allow monitoring of patterns of variation within and between the wood of annual growth increments.

Several techniques have been developed, the most important of which use gamma-rays [Parrish, 1961; Loos, 1965], beta-rays [Cameron, Berry, Phillips, 1959; Adams, Hearmon, 1962; Harris, 1969], or X-rays [Polge, 1963, 1965; Rudman, McKinnell, Higgs, 1969; Polge, Nicholls, 1972].

Wood density measurement using gamma radiation is not yet used for routine analysis, but offers interesting potential for the development of apparatus to measure a wide range of specimen size, since gamma-ray sources include a wide spectrum of penetrating power. Both the X-ray and beta-ray methods are in use for routine analysis. The major advantage of the X-ray method over the beta-ray method is the greater speed with which measures of wood density can be made [Harris, Polge, 1967; Phillips, 1968].

The X-ray method of wood density determination is described in detail by Polge [1965], Rudman *et al.* [1969], and McKinnell [1970].

A wood sample of uniform moisture content and constant thickness within the range 4 to 10 mm in the radial longitudinal plane, is irradiated parallel to the fibre alignment with low energy (soft) X-rays for a specified time. The resultant X-ray film is scanned on a double-beam recording microdensitometer to produce a continuous record of variation of optical contrast of the sample image.

The optical density of the wood sample image is a negative function of wood density, the linearity of this function being dependent upon the incident radiation spectrum and the sample thickness. Transformation of the measures of optical density to wood density values is facilitated by reference to a calibration curve. A standard calibration curve is derived by relating optical densities of the X-ray images of a large number of standard wood samples from a wide range of species to their known gravimetric densities. Working standards (step wedges), made from cellulose acetate or other suitable material and calibrated by reference to the standard curve, are irradiated with the wood samples on each film to facilitate the derivation of an individual film calibration curve for each exposure.

Output of measures of optical density from the densitometer have until recently been in the form of chart traces [Polge, 1965; Rudman *et al.*, 1969], but the development of electronic systems for conversion of the output to digital form [e.g. Echols, 1973] provide vastly increased efficiency of data handling.

Sample Preparation

The wood discs, obtained as outlined in Chapter 2, were dried at 30 °C in a kiln in a forced air flow.

A longitudinal strip 1.25 cm wide was removed using a bandsaw. This strip was located across a diameter as close as practicable, allowing for damage such as checking, to the diameter with the most symmetric radii (usually the smallest diameter). This subjective choice of radii avoided sampling the areas of compression wood which were conspicuous in some of the more highly asymmetric radii.

The diameter strip was further sawn to a depth of 1.25 cm. The four sawn faces were machined to yield a strip of approximately 10 mm × 10 mm cross section, using a Black and Decker router modified as a spindle moulder with a tungsten carbide tipped cutter. The spindle moulder used was of a similar design to the machine used by Rudman *et al.* [1969] but was constructed to allow a finer precision of adjustment and a high degree of uniformity of machined width along the length of the sample.

The diameter strips were extracted for 12 hours in benzene: ethanol (1:2) in a Soxhlet apparatus, cleared in a vacuum oven, and further routed to a thickness of 6.9 ± 0.04 mm in the radial longitudinal plane.

Samples were conditioned to 8 ± 0.5 per cent moisture content in a desiccator over a saturated solution of sodium dichromate, which has a constant aqueous vapour pressure (8 ± 0.5%) at normal ambient temperatures. The moisture content of specimens must be precisely regulated prior to X-raying as both water and wood contribute to the absorption of the X-radiation.

Analytical Procedure and Computation of Wood Density Values

The technique used to prepare films with the X-ray negative images of the wood samples was described in detail by Rudman *et al.* [1969], and McKinnell [1970].

Wood samples were aligned on a 20.3 × 25.4 cm Kodak AA brand X-ray film, not less than 4 cm from the film edge, and irradiated with X-rays from a source 2.5 m distant. All samples were X-rayed parallel to the wood grain. The X-ray source distance of 2.5 m reduces parallax errors, which may cause blurring of the grain image towards the edges of the film, to an acceptable maximum of less than 0.03 mm. The brand of film chosen was shown previously [McKinnell, 1970] to be suitable for routine use without background correction.

Samples were exposed for 7 minutes to X-rays generated by an acceleration voltage of 23 kV at 20 ma. An 0.6 mm aluminium filter was interposed 25 cm from the source to attenuate the longer wavelength radiation in the emission spectrum.

These analytical conditions were developed earlier for routine analysis of wood samples [Rudman *et al.*, 1969; McKinnell, 1970]. They provide a suitable exposure for the specified film type, and effect a satisfactory compromise between sharpness of the sample image and the linearity of the wood density:optical density calibration curve.

Cellulose acetate working standards (step wedges) were used. These were calibrated against a standard wood density:optical density calibration curve. The standard curve was calculated from measures of

the gravimetric density (oven-dry weight / volume at 8% moisture content) of a large number of standard wood samples from a wide range of species . The derivation of the standard curve is described by McKinnell [1970]. Each step wedge comprised a range of standards equivalent to 0.229, 0.344, 0.468, 0.592, 0.717, and 0.867 g/cc wood density.

Two step wedges were irradiated with the samples on each film. The wood samples were positioned on the X-ray film at random with respect to tree and disc number to minimise possible systematic error.

Each film was developed for 5 minutes and fixed for 5 minutes at 20 °C in flat trays. During developing and fixing the film was continuously turned and swept through the liquid in all directions using a gentle gliding motion. Continuous agitation is necessary particularly during developing to remove chemical by-products from the immediate vicinity of each developing grain, thus allowing uniform development throughout the sheet of film. The technique used is relatively cumbersome, and a much improved developing system is described elsewhere [Polge, Nicholls, 1972].

Following fixation, the film was washed thoroughly and dried in a forced air flow at 30 °C.

A Joyce-Loebl Mark III c.s. dual beam recording microdensitometer was used to translate the optical contrast on the X-ray film into a continuous chart recording. The dimensions of the scanning beam were kept constant at 0.18 × 1.0 mm (length:width) throughout the study to ensure that any error of estimate of optical density resulting from machine response characteristics remained constant. A tracing 5 × the actual sample size was used throughout this investigation.

On the densitometric tracings, the optical density of a sample or calibration wedge is measured as the linear displacement of the curve from an arbitrary baseline setting which is kept constant for measures of all samples and standards on a particular film. A linear correction was applied to compensate for any deviation greater than 0.04mm of the wood samples from a thickness of 0.69mm.

Mean optical density is estimated by integrating the area beneath the curve and dividing by the width of the traverse. A Joyce electronic integrator was used for this purpose. Slight variation of the rate of movement of the sample stage and tracing platform on the

microdensitometer caused an error of from 0-4% in the estimate of mean optical density by integration. The error was contained within these limits by frequent cleaning of the teflon bearings upon which the movable platforms are mounted and polishing of the surfaces over which they move.

Variation of optical contrast within an X-ray film resulting from the developing technique was kept to an acceptable maximum by rejecting any film if the variation between the optical densities of the 0.468 density level of the two step wedges exceeded 2 mm on the densitometer tracings. This resulted in a discard rate of less than 1 in every 10 films processed.

The transition between annual growth increments is typically represented as an almost vertical fall in the optical density tracing. Annual growth increments were demarcated on the tracings at the mid-point of the vertical transition. Some examples of densitometer tracings are illustrated in Figure 3.1. Correct demarcation of the annual rings is aided by similarities among trees of the pattern of density variation in increments laid down during a particular growth season.

The choice of variables for measurement on the densitometer tracings has received considerable attention in the literature [Rudman, 1968; Harris, 1969; Brazier, 1969; Nicholls, Brown, 1971; Echols, 1973]. The range of measures available to this study was restricted by the time-consuming labour involved in hand measurement of graphic tracings.

(i) Density values

The tracing of a typical annual increment is illustrated in Figure 3.1, with the more readily apparent parameters identified. Maximum density and minimum density are, respectively, the maximum and minimum values reached in the growth ring. The density range is the difference between these two values. It is an index of wood texture, and is a characteristic related to veneer peeling quality, machineability, and weathering properties of the wood. It has been shown to be related to pulp quality [Smith, Horton, 1968] and to the mechanical properties of wood [Kennedy, 1968].

Wood mean density is derived from the mean optical density, which is calculated by integrating the area beneath the curve and

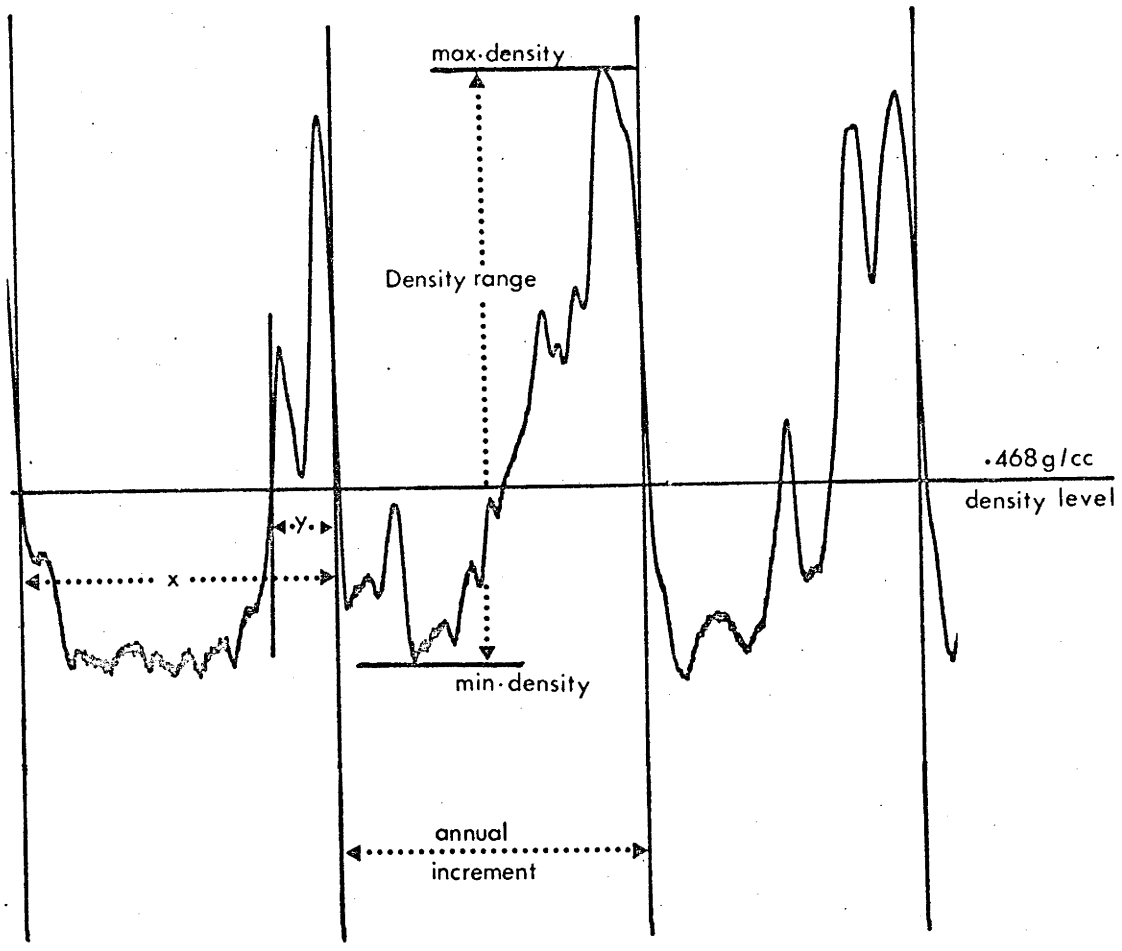


Figure 3.1: The densitometric tracing of 3 annual growth increments. from a wood sample of var. hondurensis.

dividing by the width of traverse. Mean-density is extensively used as a general index of wood quality. It is a useful index of the suitability of wood for many purposes [see, for example, Mitchell, 1964]. It is closely correlated with pulp yields and with tear resistance in the pulp [Barefoot, Hitchings, Ellwood, 1964; Dinwoodie, 1965], and has an important bearing on timber strength properties.

Calculation of the wood density values from the measures of optical density was performed by a computer programme, "WØØDENTRANS", developed for use on an IBM 360/50 computer. The optical density values corresponding with the known wood density standard values (steps) of each of the 2 calibration wedges on a particular film were averaged. The optical density measure of each sample was related to a chosen number of measures of optical density of the calibration steps nearest in value to

it, and the sample wood density estimate evaluated by polynomial interpolation or extrapolation. The number of standard reference points was generally chosen to be 3, resulting in the wood density estimate being evaluated using a cubic function. This system avoids the problem inherent, for example, in the system used by McKinnell [1970], of inaccuracy associated with the goodness of fit of a single quadratic expression to the film calibration values of optical density. The problem is potentially serious near the extremities of the calibration curve.

(ii) Indices of density variation within the annual increment

The technique of X-ray densitometry provides a continuous record of density variation measured with a high degree of resolution. This form of output facilitates the use of a range of measures to describe the distribution of density within the growth ring.

Latewood percentage [Mork, 1928] has been used as an index of density distribution within the annual increment. It has been used extensively as an index of wood quality [Edlin, 1965]. Latewood percentage has usually been measured microscopically, and its application was suited only to the measure of specimens with a sharp contrast between earlywood and latewood zones.

The advent of radiological techniques of density measurement has enabled a more objective measure of latewood percentage, and extended the application of the measure to wood specimens with a low density contrast within the annual increment; for example, the innermost rings in many conifers, including *Pinus caribaea*. Several techniques have been devised to estimate latewood percentage [Phillips, 1960; Elliot, Brook, 1967; Rudman, 1968; Harris, 1967, 1969; McKinnell, 1970; Brazier, 1969].

A new parameter, "latewood ratio", measured as

$$\text{latewood ratio} = \frac{\text{mean density - minimum density}}{\text{density range}},$$

has been used as an index of density distribution within the annual increment [Harris, 1969; Nicholls, Brown, 1971]. The latewood ratio is essentially a descriptive characteristic. It is a measure of the proportion of "latewood" in a ring assuming a linear change from

earlywood to latewood and an earlywood/latewood boundary at the mid-density point [Nicholls, Brown, 1971].

The parameters described are all suited to derivation from values obtained by hand measure on graphic tracings. Modification of the densitometer to yield taped digital output suitable for direct computer analysis can extend the range of measures of the distribution of density within the growth ring; e.g. the wood "uniformity number" [Echols, 1972, 1973] and statistical measures of intraincremental dispersion of density values [J. Burley, Oxford, pers. comm.].

In this study latewood percentage is measured as the proportion of the annual increment with a density greater than 0.468 ($\frac{y.100}{x}$ in Figure 3.1). This is an arbitrary value which lies in the transition zone from low to high density of the majority of samples used in this study. The figure corresponds with the density value of one of the calibration wedge steps. A similar value was used in a study of *Pinus radiata* [McKinnell, 1970].

All values were computed from hand measures using programme "WØØDENTRANS". The latewood ratio [Harris, 1969] was also computed.

(iii) Ring width

The radial width of the annual increment is readily measured on the densitometric tracing (see Figure 3.1). The magnification factor (1/5) was applied, and a measure of the distance from the pith to the mid-point of each growth ring was calculated from these values by programme "WØØDENTRANS".

A measure was also made of the width of latewood in each growth ring.

3.2 MEASUREMENT OF WOOD CELL DIMENSIONS

The structure of the xylem of var. hondurensis is typical of the genus *Pinus*. Imperforate tracheary elements (tracheids) are the dominant cell type. Some fibre-tracheids occur in the latewood. Axial parenchyma is scantily developed and is restricted to cells associated with resin ducts. The rays are mostly uniseriate and composed mainly of parenchyma cells.

In this study the terms fibre and tracheid are both used to describe the dominant wood elements, although the distinction between tracheary elements and fibres [Esau, 1953] is appreciated.

Tracheid dimensions are an important feature of wood from the standpoint of utilisation. Fibre length affects several strength characteristics of both wood and its derived products, particularly kraft paper [Dadswell, Wardrop, 1959; Dinwoodie, 1961]. The relationship of fibre diameter and lumen width with wall thickness has an important bearing on fibre flexibility which in turn affects a number of paper properties [Dinwoodie, 1965; Runkel, 1952].

Wood density of coniferous species is, to a large extent, determined by the amount of cell wall material in a given volume of wood [Lavers, 1967]. This is a function of tracheid diameter and wall thickness, and, to a lesser extent, tracheid length. Although tracheid diameter and wall thickness vary simultaneously, the physiological processes controlling secondary wall thickening appear to be independent of those regulating tracheid diameter [Larson, 1960; Richardson, Dinwoodie, 1960; Brown, 1970]. It follows that an understanding of the processes controlling anatomical variation is a prerequisite to maximum efficiency in breeding for wood density.

Despite the time-consuming and tedious nature of their measurement, the inclusion of measures of cell dimensions in this study seems well justified, particularly in view of the paucity of the present knowledge of the variation of cross-sectional dimensions of the tracheids and their covariation with other important wood characters in var. *hondurensis*.

(a) Tracheid length

The tracheid length in the earlywood region of selected growth rings was measured. The earlywood region was separated with a scalpel and macerated for approximately five hours in a mixture of 100 vols. hydrogen peroxide:glacial acetic acid (1:1) at 100 °C. Samples were thoroughly washed and stained with 1% saffranin, then separated in distilled water by high frequency (50 c.p.s.) vibration using a Vortex "genie" vibrator. The method causes a thorough mixing, which results in a randomised suspension of tracheids. A subsample of fibres was

extracted from this suspension by separating it on the mouth of a disposable pipette. The subsample was mounted on each of two microscope slides in (1:1) glycerol:water and the fibres separated by rapid (50 c.p.s.) vibration of the slides. Coverslips were then applied.

The slides were affixed to a specially devised mount and the fibre images projected onto a vertical screen at approximately 45 × magnification using an Aldis 35 mm slide projector. Slight distortion of the projected image occurred towards the edges of the screen. Each slide was scanned systematically, and the length of the projected images of unbroken fibres was measured to the nearest millimetre on the central part of the screen with a map tracing wheel.

Some errors associated with the measurement of tracheid length, and the derivation of formulae for estimating the precision of measurement are discussed in detail elsewhere [Tappi, 1966; Harris, 1966; Burley, Burrows, Pattinson, Press, 1967; Davidson, 1972]. Two hundred fibres in each of four samples were measured individually to obtain an estimate of the number of samples required to estimate the mean fibre length to within specified percentages of the slide population mean using the formula

$$n = \left(\frac{c.t}{e}\right)^2$$

where n = number of individual measurements required,

c = coefficient of variation of the measurements,

t = the normal deviate (= 1.96 for 95% confidence with a sample size of roughly 100 or more),

e = error % of the mean required.

This somewhat limited test indicated that approximately 16 and 42 fibres respectively, are required to obtain an estimate of the mean fibre length to within 5% (0.23 mm) and 3% (0.14 mm) of the slide population mean (4.5 mm).

More extensive measurement of tracheid length in tropical pines has indicated that the mean of 50 tracheids gives adequate precision in routine sampling [Burley *et al.*, 1967; Burley, Adlard, Waters, 1970].

A measure of the projected images of 25 fibres on each of two slides (total 50 fibres) was made on each sample. Computation of the mean fibre length of each sample from these data was carried out on the IBM 360/50 computer using a programme, "WØØDCELLS", which was developed to facilitate the calculation of all the cell dimensions measured in this study.

(b) Tracheid wall thickness and lumen diameter

The radial cross-section dimensions of the tracheids were measured separately in both the earlywood and latewood regions of selected growth rings.

Growth rings selected for measurement were separated and the cross-sectional surfaces, machined for use in the X-ray densitometric study, were further smoothed in a sliding microtome and stained with a 1% aqueous solution of malachite green:methylene blue (1:1) in preparation for examination by reflection microscopy. The specimens were examined under water using a Leitz Ultrapack Reflection microscope mounted on a dual linear traverse measuring micrometer. An overall magnification of 687.5 × was provided by a 55 × water immersion objective, a 1.25 × intermediate stage, and a 10 × stereoscopic occular with cross hairs. A high intensity Xenon arc lamp was used to provide illumination.

The technique of cell measurement using this instrument is discussed in detail elsewhere [Smith, 1965].

A precision of 0.5 μ on individual measurements was considered adequate. The limit of resolution by visual light microscopy is approximately 0.2 μ under optimal conditions [Smith, 1965].

A sample size of 40 was shown to yield an estimate within 5% of the mean sample value of both double wall thickness and lumen diameter on four sets of individual measures of 100 cells, using reasoning similar to that used for tracheid length.

Cumulative measures of the thickness of the two walls of adjoining cells (double wall thickness) and of the diameter of the cell lumens were made separately in the latewood and earlywood regions.

Since the single cut on the sample surface intersects the tracheids randomly with respect to their length, measures of contiguous

cells in the radial direction gives statistically reliable means. In order to increase the precision with which the mean cell dimensions are estimated by a given sample size, tracheids which appeared to have been sectioned towards the extremities were not measured.

Two sets, each of 25 cells (total 50 cells) were measured in each of the earlywood and latewood zones of the selected growth rings. Each set comprised measures of cells from at least 3 radial files which were selected at random.

CHAPTER 4

FEATURES OF THE WOOD: THE VARIATION AND ASSOCIATION OF WOOD CHARACTERS AND THEIR INTER-RELATIONSHIPS WITH SOME INDICES OF TREE GROWTH, MORPHOLOGY, AND NUTRITION

4.1 EXPERIMENTAL MATERIAL AND METHODS

(a) Experimental Material

The experimental material was sampled in early December, 1970, from a routine planting of var. *hondurensis* of approximately 4 hectares (10 acres) established at Beerburrum Forest (Compartment 14; Wild Horse) in southern coastal Queensland (26° 58' S, 153° 00' E; altitude approximately 36 m) in February, 1953.

The plantations of exotic conifers are established on areas that formerly carried low quality eucalypt forest (locally called "wallum" in the broad sense). The broad soil groups and ecology of the region have been described by Coaldrake [1961]. The soils of the area are derived predominantly from Mesozoic sandstone overlayed by Quaternary sands. The local soil variations and groups have been described by Vallance [1938] and by Pegg [1967]: The latter in relation to the growth of slash pine (*Pinus elliottii* var. *elliottii*), which is grown extensively in the region.

The sample stand is established on a lateritic podzolic soil type that in texture may be described as a coarse loamy sand. There is little topographic relief in the surrounding country. The site sloped very gently towards an uncultivated swamp. The soil of the major part of the stand was apparently freely drained, with a ground cover of grasses and *Xanthorrhoea* spp., but towards the periphery of the stand, in the direction of the swamp, sedges (*Ghania* spp.) entered the ground flora, and increased to predominate the ground cover, with *Xanthorrhoea* spp. absent, towards the swamp edge of the stand. The sedges are indicative of soil water impedance resulting in waterlogged conditions in the upper layers of the soil for at least part of the year. In areas where sedges

dominated the ground cover tree growth was noticeably stunted, and the foliage chlorotic, relatively sparse, and of "littleleaf" appearance. The sample "plots" were located in areas of the stand well removed from the locations in which sedges occurred in the ground cover. It is, however, possible that soil drainage of the plots may be somewhat impeded seasonally.

Some climatic data for the area are presented in Figure 4.1.

Stand History

The vegetation of the site prior to cultivation comprised eucalypt woodland, with species including *Eucalyptus pilularis* (blackbutt), *E. microcorys* (tallowwood), *E. intermedia* (bloodwood), *E. gummifera*, *E. micrantha*, *Melaleuca* spp., and *Acacia* spp. Site preparation comprised mechanised clearing: The vegetation was pushed into localised heaps and burned.

Tubed stock of var. *hondurensis* (of seed source Batch 4, from Mt. Pine Ridge, British Honduras) were planted in February, 1953, at spacing 2.4 m × 2.4 m (8 ft × 8 ft). Fertilisation history comprised the application of rock phosphate at 314 kg/ha (2.5 cwt/acre) in 1959. The stand was thinned precommercially to 990 stems per hectare (400 stems per acre) in February, 1958, and to 740 s.p.ha. (300 s.p.a.) in January of 1960. Thinning was, in general, directed towards retaining the better stems. A merchantable thinning in February, 1970, reduced the stand density to 445 s.p.ha (180 s.p.a.).

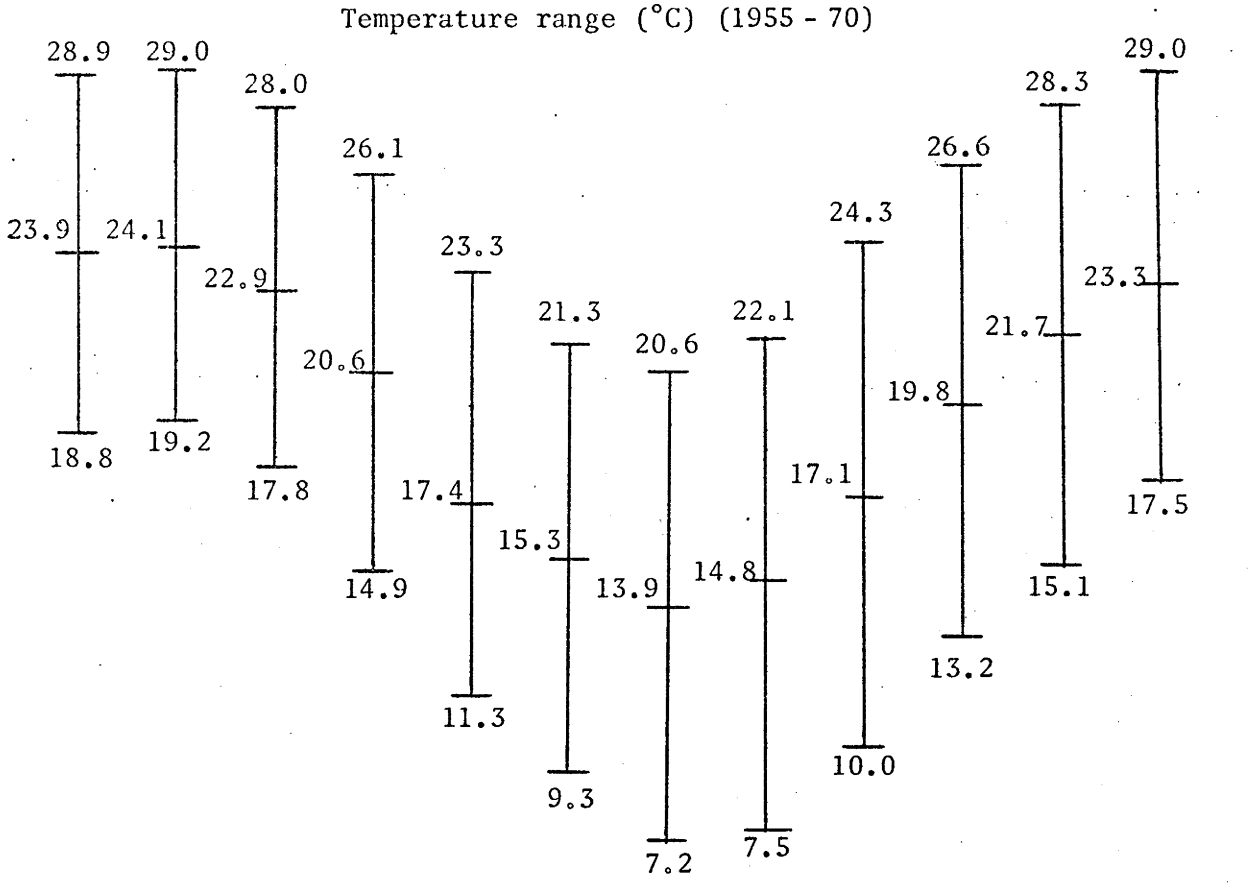
(b) Experimental Methods

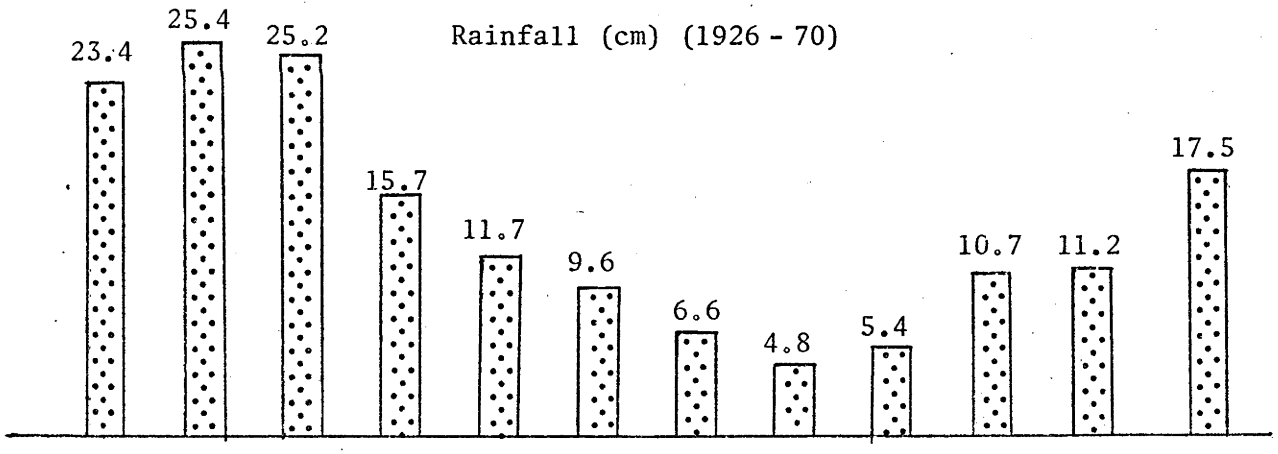
Two "plot" areas (referred to subsequently as plots A and B) were chosen at random within the confines of the stand that were well removed from areas showing evidence of internal soil-water impedance (see above) and at least 8 rows (20 m = 64 ft) from the periphery of the stand. Ten trees were chosen from each "plot" by ranked-set sampling (Chapter 2); ranking on stem diameter at breast height (1.3 m), and using a set size of 10.

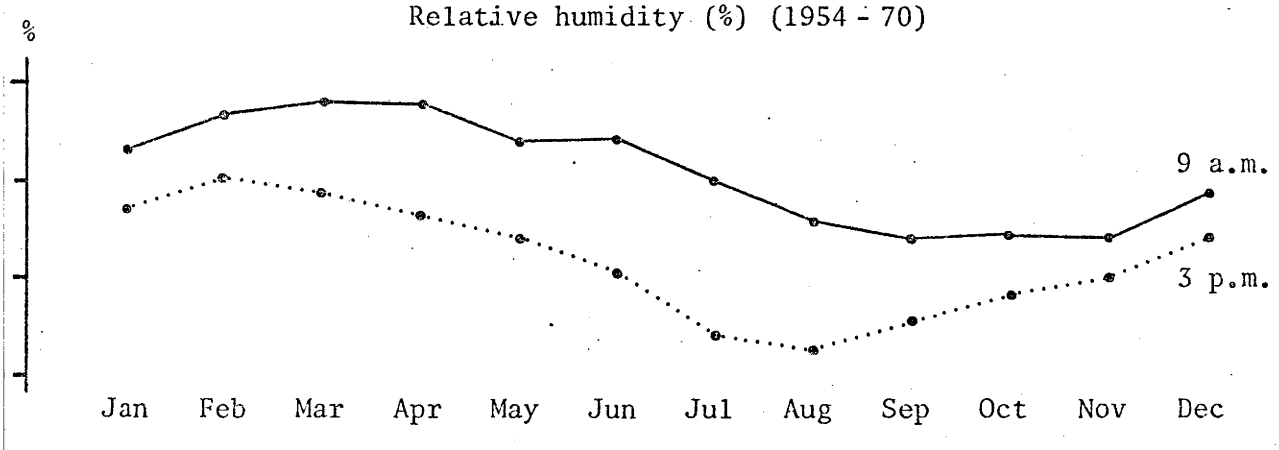
Samples of wood, foliage, and soil were extracted in accordance with the techniques described in Chapter 2.

Figure 4.1: Summary of the seasonal patterns of variation of temperature rainfall, and relative humidity for the Beerwah/Beerburrum area (extracted from records of the Queensland Department of Forestry).

The figures represent mean values (for the periods indicated) of the monthly averages of daily recordings.


Temperature range (°C) (1955 - 70)
28.9
23.9
18.8
29.0
24.1
19.2
28.0
22.9
17.8
26.1
20.6
14.9
23.3
17.4
11.3
21.3
15.3
9.3
20.6
13.9
7.2
22.1
14.8
7.5
24.3
17.1
10.0
26.6
19.8
13.2
28.3
21.7
15.1
29.0
23.3
17.5


Rainfall (cm) (1926 - 70)
23.4
25.4
25.2
15.7
11.7
9.6
6.6
4.8
5.4
10.7
11.2
17.5


Relative humidity (%) (1954 - 70)
%
9 a.m.
3 p.m.
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

The preparation and laboratory analyses of these samples are described in Chapter 3 and Appendix 2 for wood and foliage/soil samples respectively.

Methods of data manipulation and analysis are discussed in relation to their application in the sections that follow.

4.2 INTER-RELATIONSHIPS AMONG WOOD CHARACTERS

(a) Introduction

The structure (i.e. the proportion and arrangement of tissues) and associated characteristics of the wood vary considerably within a species. Some of this variation may result from the response of wood formation to differences in the environments in which the trees are grown. Much of the inherent variation of wood characters is manifest as apparently random genetic differences between trees and as patterns of variation within trees which are partly random and partly systematic.

A study of the variation of wood properties within and between trees involves an assessment of many different characters. The inter-relationships among these characters may be varied and complex. The relationships may differ in kind and degree within or among trees or populations of trees. They may be predictable from hypothesis, but are usually imperfectly known.

In a study of the variation of a series of wood characters, the analysis of the set of measures of the characters may be approached in either of two ways: (i) The variation of each variable may be examined in isolation, or (ii) the variation and covariation among a set of several variables may be analysed simultaneously. The former, or univariate, methods may be used to estimate the patterns of variation of individual characters and are particularly appropriate where these each have unique importance.

Multivariate statistical techniques can be used effectively in the identification and estimation of relationships among variables and in the investigation of patterns of variation within a heterogeneous population. Their use is particularly appropriate to the analysis of data sets involving many variables, where a subjective assessment of the variation and covariation among the variables would result in the discard

of much of the information content of the original sample measures. Multivariate analytical techniques may also provide an efficient summarisation of a complex data set; i.e. the apparent dimensionality of variation and covariation may be simplified. This is achieved either by expressing most of the variation among several variables as that in a smaller number of linear combinations of the variables, or by demonstrating the effective redundancy of those variables that do not contribute significantly or uniquely to the overall variation in the data set.

Although much of the mathematical theory required in the construction of multivariate models has long been available, only recently, with the advent of electronic computers, have these models been applied in the general field of ecology. The relatively few reported applications of multivariate statistical techniques in Forest Science have been reviewed recently [Andrew, 1972]. Numerous descriptions and evaluations of the range of multivariate models and their application are available [e.g., Seal, 1964; Orloci, 1966, 1968; Cassie, 1969; Cooley, Lohnes, 1971; Andrew, 1972].

In this study a metric model, namely principal component analysis,* is used to identify and estimate the relationships among variables. In this regard the technique is of value primarily in the generation rather than testing of hypotheses. Examination of the patterns of variation of individual characteristics complements the study of the variation among the variables by effecting some estimate of their likely function within the universe of measured characters.

(b) Data Sets

The complete data set comprises measures made within annual growth increments at selected height levels of 15 wood characters [Table 4.1].† The reference numbers allocated to each wood character are retained throughout the presentation of the statistical analyses.

Measures of wood characters 1 to 8 (by X-ray densitometry) were made at each growth ring in each of two radii at six height levels in

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* A description of the technique of principal component analysis is presented in Appendix I.

† An additional loose copy of this table is located inside the rear cover for ease of reference.

Table 4.1: Identification of wood character variables.

Reference	Wood character
1	Maximum density (DMAX)
2	Minimum density (DMIN)
3	Mean density (DEN)
4	Density range (DR)
5	Ring width (RWID)
6	Latewood percentage (% LW)
7	Latewood width (radial width - mm) (LWID)
8	Latewood ratio (LR)
9	Latewood cell wall thickness (LWW)
10	Latewood cell lumen diameter (LWL)
11	Earlywood cell wall thickness (EWW)
12	Earlywood cell lumen diameter (EWL)
13	Latewood cell diameter (LWCD)
14	Earlywood cell diameter (EWCD)
15	Tracheid length (LFIB)

twenty trees according to the sampling scheme and analytical techniques described previously (Chapter 2). This raw data array comprises the measures of 8 different variables at 2402 sample locations. The value of each variable in corresponding growth rings was averaged for the 2 radii at each height level, and the mean ring value is used in the subsequent analyses.

Measures of wood characters 9 to 15 (tracheid dimensions) were made at the 3rd, 7th and 11th annual ring from the bark in one radius at each of the 6 height levels in which these rings occur.* In most of the trees measured, all 3 rings occurred at breast height, 10%, and 20% of tree height, rings 3 and 7 at 40%, and ring 3 only at 60% and 80% of tree height. Wood characters 9 to 14 (tracheid radial C.S. dimensions) were measured in 20 trees, yielding a 14 (variables) × 256 (sample locations)

* In some cases the innermost of these rings were present (detected on the densitometer tracings) but were excluded from the sample since visual identification of the ring boundaries was insufficiently accurate.

data set. Tracheid length (character 15) was measured in the 10 trees of sub-plot A (see subsection 4.1) which comprised 128 sample locations.

(c) Analyses and Results

Several sources of heterogeneity may be identified within the samples; in particular the systematic effects of height, and position in the cross-section, and the random variation between trees. The effects are integrated in the present section, where the overall variation in the wood is examined; i.e. no attempt is made to structure the data on *a priori* consideration of variation within the samples.

The data may be partitioned into 3 groups of variables (variables 1 - 8, 1 - 14, and 1 - 15) on the basis of their representation in different numbers of samples. Each of these data sets is analysed separately.

Mean values for the variables in each data set are presented in Table 4.2.

Pearson's product-moment correlation coefficient, r, is used as an index of affinity between each wood character pair. The correlation coefficients are maximum likelihood estimates for the population when the frequency distributions of the variables approximate the normal (Gaussian) distribution. Sample estimates of the Kolmogorov-Smirnov statistic, D_{max}, and the moment statistics γ_1 and γ_2 [Sokal, Rohlf, 1969] were computed for the variables (transformed and untransformed) in each data set to test for non-normality, using computer routines developed by Sokal and Rohlf [1969]. Appropriate transformations were applied to variables where the frequency distribution deviated from the normal distribution at the 95% confidence limit (Table 4.2).

The matrices ($\underline{R}^A$, $\underline{R}^B$, $\underline{R}^C$) of correlation coefficients for each wood character pair, derived from the 3 data sets A, B, and C are presented in Tables 4.3 A, B, and C, respectively. The matrices have been ordered to correspond with the respective principal component arrangements (Tables 4.4 A, B, C).

The correlation matrices show, in a fairly compact and simple form, the similarities and differences between the distribution of each of the wood character variable pairs. In computing the correlation

Table 4.2: Mean values and standard deviations of wood characters in 3 data sets (A, B, C). Transformations, and parametric estimates of the transformed variables, where applicable, are indicated.

Variable	Units of measure-ment	Transformation	Data set											
			A (1201 samples)				B (256 samples)				C (128 samples)			
			Arith. mean	s.d.	Transf. mean	s.d.	Arith. mean	s.d.	Transf. mean	s.d.	Arith. mean	s.d.	Transf. mean	s.d.
1 (DMAX)	g/cc		.760	.205			.749	.197			.773	.183		
2 (DMIN)	g/cc	log e x	.348	.042	-1.06	.114	.354	.042	-1.045	.115	.355	.037	-1.04	.103
3 (DEN)	g/cc	$\sqrt{x}$	.489	.089	.696	.064	.502	.097	.705	.069	.509	.091	.710	.065
4 (DR)	g/cc		.411	.192			.395	.176			.419	.167		
5 (RWID)	mm		6.95	2.94			7.17	2.74			7.23	2.69		
6 (% LW)	per cent	arcsine($\sqrt{x}$/100)	35.2	23.9	34.8	17.4	37.9	25.9	36.1	19.1	39.6	24.5	37.6	17.3
7 (LWID)	mm		2.00	1.27			2.29	1.59			2.53	1.67		
8 (LR)	ratio		.362	.123			.385	.116			.378	.118		
9 (LWW)	microns						15.68	3.64			15.73	3.38		
10 (LWL)	microns	$\sqrt{x}$					21.39	7.13	4.56	.74	20.72	6.23	4.50	.67
11 (EWW)	microns	$\sqrt{x}$					8.61	1.38	2.93	.23	8.46	1.54	2.90	.25
12 (EWL)	microns						48.8	6.72			46.6	6.06		
13 (LWCD)	microns						37.1	5.86			36.5	5.18		
14 (EWCD)	microns						57.4	7.18			55.1	6.39		
15 (LFIB)	microns										4.481	.715		

Table 4.3 (A, B, C): Correlations among wood characters. The matrices R^A, R^B, and R^C (presented in Tables A, B, and C) are derived from the data sets A, B, and C respectively.

Table 4.3 A

3 (DEN)							
6 (% LW)	87						
1 (DMAX)	77	68					
4 (DR)	66	56	98				
2 (DMIN)	72	76	43	30			
7 (LWID)	59	63	58	56	30		
8 (LR)	27	10	-31	-37	16	-01	
5 (RWID)	-58	-62	-37	-27	-59	03	-19
	3 (DEN)	6 (% LW)	1 (DMAX)	4 (DR)	2 (DMIN)	7 (LWID)	8 (LR)

Table 4.3 B

	DEN	DMAX	% LW	DR	LWW	DMIN	LWID	EWW	EWCD	LR	EWL	LWCD	RWID	LWL
3 (DEN)		**	**	**	**	**	**	**	NS	**	NS	**	**	**
1 (DMAX)	87		**	**	**	**	**	**	NS	*	NS	**	**	**
6 (% LW)	89	81		**	**	**	**	**	NS	NS	NS	**	**	**
4 (DR)	79	98	73		**	**	**	**	**	**	NS	**	**	**
9 (LWW)	72	76	66	74		**	**	**	**	NS	**	NS	**	**
2 (DMIN)	73	58	74	40	46		**	**	*	NS	**	**	**	**
7 (LWID)	64	59	70	59	55	29		**	NS	**	NS	NS	NS	**
11 (EWW)	43	40	40	34	52	44	33		**	NS	**	NS	**	**
14 (EWCD)	00	12	-04	16	35	-15	03	43		*	**	**	NS	NS
8 (LR)	29	-15	09	-18	-02	07	17	02	-16		**	NS	NS	NS
12 (EWL)	-09	04	-12	11	27	-25	-03	26	98	-18		**	NS	*
13 (LWCD)	-43	-44	-43	-40	-08	-40	-05	05	35	03	37		**	**
5 (RWID)	-60	-54	-61	-45	-42	-64	00	-22	05	-06	10	45		**
10 (LWL)	-73	-75	-69	-70	-57	-59	-30	-24	10	03	16	86	61	
	3	1	6	4	9	2	7	11	14	8	12	13	5	10

Table 4.3 C

	DMAX	DEN	% LW	DR	LWW	DMIN	LFIB	EWW	LWID	EWCD	EWL	LR	LWCD	RWID	LWL
1 (DMAX)		**	**	**	**	**	**	**	**	**	**	NS	**	**	**
3 (DEN)	82		**	**	**	**	**	**	**	NS	NS	**	**	**	**
6 (% LW)	76	87		**	**	**	**	**	**	NS	NS	NS	**	**	**
4 (DR)	98	75	67		**	**	**	**	**	**	**	*	*	**	**
9 (LWW)	76	70	62	73		**	**	**	**	**	**	NS	NS	**	**
2 (DMIN)	52	68	74	34	45		**	**	*	NS	*	NS	**	**	**
15 (LFIB)	53	50	48	48	45	42		**	NS	**	**	NS	NS	**	**
11 (EWW)	46	48	49	41	58	45	29		**	**	NS	NS	NS	*	**
7 (LWID)	56	65	70	57	51	22	11	38		NS	NS	*	NS	NS	*
14 (EWCD)	38	13	10	44	48	-07	42	33	12		**	**	NS	NS	NS
12 (EWL)	29	02	-02	36	36	-19	37	09	04	97		**	NS	NS	NS
8 (LR)	-17	34	12	-21	03	09	-07	-01	21	-37	-38		NS	NS	NS
13 (LWCD)	-28	-32	-35	-21	-01	-42	-15	-01	09	17	17	-00		**	**
5 (RWID)	-38	-48	-51	-27	-31	-67	-57	-22	16	01	07	-06	45		**
10 (LWL)	-64	-64	-63	-57	-55	-61	-39	-32	-18	-12	-04	01	84	56	
	1	3	6	4	9	2	15	11	7	14	12	8	13	5	10

coefficients the variables are adjusted to zero means and standardised (i.e. the variance of each variable is made equal to unity). Standardisation removes the quantitative effect attributed to the measurement of different variables on differing, and arbitrarily related, scales or dimensions; i.e. it eliminates the effect of differences in absolute variability among variables.

Twenty-six of the 28 correlations between the variables in $\underline{R}^{A}$ (Table 4.3A) are significant at the 1% level. The relative sizes of the coefficients are perhaps better criteria of similarity than is strict statistical significance, particularly in view of the large number of degrees of freedom. Many of the coefficients are of a high order of magnitude.

A high degree of inter-correlation among the larger range of wood character variables in $\underline{R}^{B}$ and $\underline{R}^{C}$ (Tables 4.3 B,C) is evident. When these matrices are partitioned (broken lines in Tables 4.3 B,C) the correlation coefficients in the upper left and lower right submatrices tend to be high-positive, and those in the remaining submatrices low-positive or negative. Inter-correlation among many of the densitometric characters (excluding latewood ratio) is of a high order. The very strong correlation (.87 - .89) of wood mean density with latewood percentage was noted also by Lantican [1972] in a study of 30 year-old trees of var. *hondurensis* from a natural stand at Mt. Pine Ridge, British Honduras. It is of practical significance, since it indicates that wood mean density may be predicted with high precision from the generally more easily made measures of latewood percentage.

The tracheid dimensions, excepting earlywood tracheid lumen and cell diameters, are, in general, highly correlated with the densitometric characters. These inter-correlations are of a particularly high order with latewood tracheid wall thickness and lumen diameter. A close association between annual ring width and many of the other wood characters is apparent.

The demonstration of association between wood characters is of importance *per se* in characterising the properties of the wood, but does not in itself provide an insight into underlying causal mechanisms. Correlations among variables may arise through any one, or combination of, the following mechanisms: (a) direct causal effect, (b) co-response to a

common influence, or (c) variables, to some extent, measuring the same feature.

A summary of the highest-order correlations ($r > 0.5$) is presented as an association diagram in Figure 4.2. Two groups of high-positively associated characters are apparent (Figure 4.2). Each of the characters of one group are negatively correlated with those of the other group (Table 4.3C).

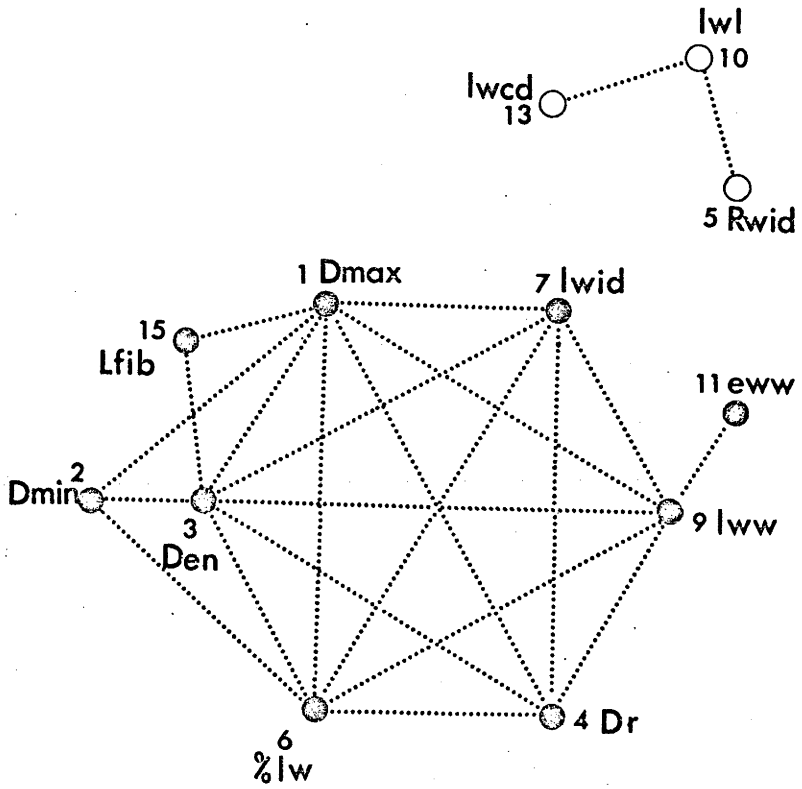


Figure 4.2: Diagrammatic representation of the association of wood characters. Only positive association is shown. The dotted lines between characters represent very strong positive correlation ($r = \geq 0.5$) between the 2 characters.

Association diagrams have been used by a number of workers to detect groups of ecologically related species [e.g. Welch, 1960; Agnew, 1961]. The diagrams facilitate, to some degree, the presentation of a large amount of information in a form that is readily appreciated. They are limited, however, in that they simply present the data; the limited element of simplification is introduced at the expense of a considerable loss of information contained in the correlation matrices, and the

technique introduces no generalisations in relation to the overall variation in the data set.

The principal components* of each of the 3 sets of variables have been calculated from the standardised data of the correlation matrices $\underline{R}^A$, $\underline{R}^B$, and $\underline{R}^C$.

The first 5 latent roots, λ, and vectors, f, for each set of variables are shown in Tables 4.4 A, B, and C. In each table the variables (wood characters) have been arranged in descending order of the elements (f-values) in the first vector. The f-values, or factor loadings of the principal components on each of the variables, are simple coefficients of correlation between the principal components and the respective variables, and have been scaled to be directly comparable between vectors. The largest absolute vector element (factor loading) for each variable is underlined. A similar form of presentation is used in subsequent analyses.

In each of the analyses a major part of the variation among the variables is summarised in the form of a relatively small number of mutually independent (orthogonal) linear combinations of the variables (components).

Approximately 90% of the information content of the respective correlation matrices ($\underline{R}^A$, $\underline{R}^B$, $\underline{R}^C$) is accounted for by 3 components of the first variable set (A: variables 1 - 8) and by 5 components of each of variable sets B (1 - 14) and C (1 - 15). The variance of each of the remaining components is less than unity, i.e., is less than the variance of the individual variables, and the affinity of individual variables with each of these components is low. This residual 10% of the information, although not non-significant in the statistical sense (i.e., most of the λs can be differentiated from one another) may be rejected since it is exceedingly difficult to interpret in the context of wood structure or biology.

In geometric terms, the hyperspace of wood character measures is now reasonably faithfully described by a relatively small number of principal axes corresponding with the principal components z_{1-3} for variable set A and z_{1-5} for each of sets B and C (see Appendix 1).

---

* A description of the technique of principal component analysis is presented in Appendix 1.

Table 4.4: Principal components of wood characters. The components extracted from the standardised measures of data sets A, B, and C are presented in Tables 4.4 A, B, and C respectively.

Table 4.4 A

Principal component	z_1	z_2	z_3	z_4	z_5
λ (variance of corresponding component)	4.45	1.71	0.94	0.53	0.26
Percentage of total variance	56	21	12	7	4
Cumulative percentages	56	77	89	95	99
Variable					
3 (DEN)	94	20	12	-13	15
6 (% LW)	92	18	05	17	-19
1 (DMAX)	88	-41	-11	-16	12
4 (DR)	79	-54	-08	-27	08
2 (DMIN)	72	44	-13	49	24
7 (LWID)	66	-29	62	16	-22
8 (LR)	-00	80	47	-35	08
5 (RWID)	-60	-50	53	18	27

In the analysis of variable set A (1 - 8) the first component alone accounts for more than half (56%) of the total variation in the standardised data set. The component is associated positively with the densitometric features other than the latewood ratio, with which it has no affinity. It is strongly correlated with the contrast between latewood percentage and ring width, i.e., with growth rate and the resultant relative proportions of different types of wood tissue. In the interpretation of this component the suggestion that the growth rate factor may be an important causal mechanism underlying the major axis of variation is supported by the individual simple correlations of ring width with 5 of the densitometric variables (mean density, latewood percentage, maximum density, density range, and minimum density — Table 4.3), all of which are negative and highly significant. An alternative interpretation is that this linear combination of variables

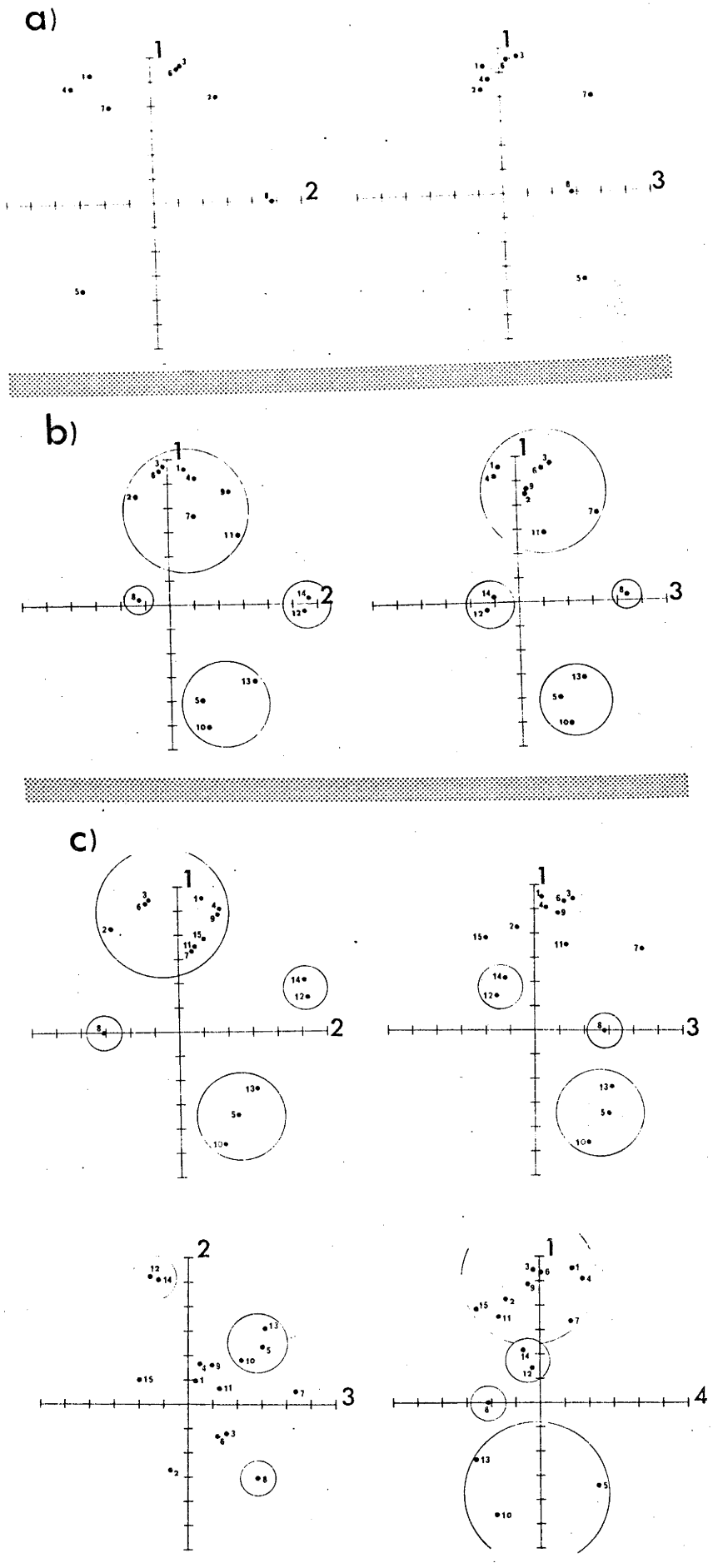
is a response to the systematic variation of the variables associated with position in the stem cross-section. Either or both of these interpretations is tenable: It is difficult to estimate the relative importance of growth rate and "age" since the variation of ring width and many of the densitometric features is approximately co-linear with ring number (see subsection 4.5, wherein the effects of 'age' and radial growth rate are isolated).

The second component, z_2, accounts for 21% of the variation of $\underline{R}^A$. It is strongly correlated with the latewood ratio; an index of intra-incremental density distribution independent of the density scale. The component is independent of the absolute value of the density of the complete annual rings and of the variables that estimate within-ring density distribution with respect to the density scale (i.e. latewood percentage and latewood width). z_2 has a moderate negative affinity with an index of intra-incremental texture (i.e. within-ring density range) and the loadings on ring maximum density (-ve) and ring minimum density (+ve) are moderate. The moderate negative correlation of ring width with z_2 ($r = -0.60$) suggests an effect of growth rate upon the aspect of variation among these densitometric features expressed by the component. The interpretation of the second component is more difficult than that of the first. z_2 represents a considerable element of the total variation of the densitometric properties of the wood: It is important in characterising these properties, and the mechanisms underlying this variation are presumably of considerable biological significance.

The third component, z_3, accounts for 12% of the variation of $\underline{R}^A$. The component is characterised by its positive affinity with ring width and with latewood width and latewood ratio, and the lack of affinity of the component with the other densitometric features. It is difficult to interpret.

The overall affinity of the variables with each of the major principal components is more readily appreciated by reference to 2-dimensional scatter diagrams of the components against one another (Figures 4.3 a, b, c). The factor loadings (f-values) are the co-ordinates of each of the variables on the principal components.

Groupings of variables that have similar affinities with the principal axes of variation of the variable set are apparent. One may


a)
b)
c)

advance the hypothesis that the constituent characters of each character grouping either: (a) have a certain element of common response to causal mechanisms underlying the principal gradients of variation among the characters, or (b) are causally inter-related by the direct influence of one or more characters upon the other(s).

The principal compoents of variable sets B (1 - 14) and C (1 - 15) are similar in many respects (Tables 4.4 B,C).

The first component, z_1, accounts for just under half (47% and 44%) of the information content of the respective correlation matrices $\underline{R}^B$ and $\underline{R}^C$.

The correlations of each of the densitometric variables with z_1 presents a pattern of affinity essentially similar to that of the corresponding vector extracted in the analysis of the densitometric features alone (variable set A — Table 4.4A). z_1 is strongly correlated with the contrast between latewood tracheid wall thickness (+0.78, +0.81) and latewood tracheid lumen diameter (-0.84, -0.77), but the affinity of the component with the latewood tracheid diameter (-0.53, -0.39) is low to moderate. Earlywood tracheid wall thickness has its highest loading on this component, but the correlation (+0.48, +0.59) is relatively weak. Earlywood tracheid diameter (+0.04, +0,36) and lumen width (-0.05, +0.24) each have a low to negligible affinity with z_1. The loading of z_1 on earlywood tracheid length (+0.64) is high.

As with the first component extracted from variable set A (densitometric features alone), z_1 is strongly correlated with the contrast between latewood percentage and ring width. The sampling schedule on which the data sets B and C are based (see section 4.2b) may have reduced the effect (cf. data set A) of systematic variation of the variables associated with position in the stem cross-section, but even so this may be an important influence underlying the variation expressed by the first component.

The demonstration of the major trend of simultaneous variation among the densitometric characters and the wood cell dimensions introduces valuable resolution to the characterisation of the wood, and provides a sound basis for hypothesis of the functional interaction of the wood characters.

Table 4.4 B

Principal component	z_1	z_2	z_3	z_4	z_5
Eigenvalue (λ)	6.58	2.70	1.41	1.09	0.79
Percentage of total variance	47	19	10	8	6
Cumulative percentage	47	66	76	84	90
Variable					
3 (DEN)	95	-03	23	05	-12
1 (DMAX)	93	11	-12	-22	-00
6 (% LW)	92	-06	17	-02	06
4 (DR)	87	18	-15	-34	-09
9 (LWW)	78	41	07	-04	01
2 (DMIN)	75	-22	06	38	35
7 (LWID)	61	17	54	-47	01
11 (EWW)	48	47	18	33	40
14 (EWCD)	04	94	-17	18	-18
8 (LR)	04	-21	73	38	-52
12 (EWL)	-05	91	-22	13	-27
13 (LWCD)	-53	57	43	01	26
5 (RWID)	-66	21	26	-50	03
10 (LWL)	-84	25	33	-01	20

Table 4.4 C

Principal component	z_1	z_2	z_3	z_4	z_5
Eigenvalue (λ)	6.64	2.77	1.82	1.06	0.81
Percentage of total variance	44	18	12	7	5
Cumulative percentage	44	63	75	82	87
Variable					
1 (DMAX)	92	16	05	22	-01
3 (DEN)	91	-20	26	-04	19
6 (% LW)	89	-22	20	01	-03
4 (DR)	85	28	08	29	05
9 (LWW)	81	27	16	-08	-07
2 (DMIN)	71	-45	-12	-23	-25
15 (LFIB)	64	17	-33	-43	21
11 (EWW)	59	11	21	-28	-53
7 (LWID)	56	09	73	21	06
14 (EWCD)	36	85	-20	-11	10
12 (EWL)	24	87	-26	-05	24
8 (LR)	-00	-51	47	-35	53
13 (LWCD)	-39	52	52	-44	-12
5 (RWID)	-57	39	50	39	-01
10 (LWL)	-77	30	36	-30	-07

The close association of annual ring mean density and latewood percentage and their contrast with ring width may result, to some degree, from the influence of annual growth rate on the relative proportion of thick-walled "latewood" tissue in the growth ring. The very strong correlation of z_1 with the contrast between tracheid wall thickness and lumen width in the latewood indicates that the amount of cell wall material per unit volume of wood (i.e., proportion of wall material to void) in the latewood region is the anatomical characteristic that most influences the variation of the absolute values of these densitometric characteristics. The width of the latewood tracheids has considerably less influence, but the moderate negative association of z_1 with latewood tracheid diameter indicates that this character is associated with the major gradient of variation among the measured wood characters. Within this gradient, the larger diameter latewood tracheids tend to have wider lumens and narrower walls.

The very strong association of ring maximum density with the contrast of wall thickness and lumen width in the latewood cells is readily amenable to hypothesis: Maximum density always occurs in the latewood region of the annual increment, and its response to the relative proportion of wall material and void is theoretically predictable.

The close association of ring minimum density with the latewood cell characteristics presumably results from a common response to a position effect. There is a systematic trend of increase in minimum density (and also of maximum and mean density, latewood percentage, and tracheid cross-sectional dimensions) with ring number from the pith (see section 4.3). Thus, minimum density tends to be highest in regions of the wood where the values of mean and maximum density are also high. The common association of earlywood tracheid wall thickness and minimum density with z_1 could be an expression of direct causal effect. The low affinity of the lumen width and cell diameter of the earlywood tracheids with z_1 suggests that these anatomical characteristics have less influence than tracheid wall thickness on the lowest density values in the earlywood. The simple product-moment correlations of minimum density with earlywood tracheid wall thickness (+0.55**, +0.45**), lumen diameter (-0.25**, -0.19*), and cell diameter (-0.15*, -0.07 NS) support this interpretation.

Intra-incremental density range tends to be greatest simultaneously with highest values of both maximum and minimum density. The variation of density range is most strongly influenced by changes in the value of ring maximum density; these changes being greater and more variable both within trees and between trees than those of ring minimum density (see section 4.3).

The close affinity of the variation of earlywood tracheid length with the principal gradient of variation among the 15 measured wood characters could reflect, to some extent, co-response to systematic variation with position in the stem cross-section. The strong correlation of z_1 with the contrast between tracheid length and ring width (Table 4.4C) and the high zero-order negative correlation (-0.57**) of ring width and tracheid length (Table 4.3C) may reflect a response of variation of tracheid length to growth rate. Bannan [1954, 1955, 1956] has shown that in circumstances favourable for growth, frequent periclinal divisions in the cambium encourage earlier pseudotransverse divisions of the fusiform initials and, hence, production of shorter tracheids. A possible, though presumably relatively minor effect of tracheid length on the densitometric characters, resulting from the influence of tracheid length on the amount of cell wall material in a given volume of wood, is consistent with the relationships demonstrated. Tracheid length in the latewood region of the annual increment was not measured. Many investigators [e.g. Bissett, Dadswell, 1950; Taras, 1965; and see review of Dinwoodie, 1961] have shown that, within a growth ring, tracheids are generally larger (up to 30%) in latewood than in earlywood (but cf. a report of consistent decrease in tracheid length in single rings of young loblolly (*Pinus taeda*), slash (*P. elliottii*), and shortleaf (*P. echinata*) pines [Jackson, Morse, 1965]).

The second component, z_2, accounts for 19% and 18% of the variance of the respective correlation matrices $\underline{R}^B$ and $\underline{R}^C$. The variable loadings on z_2 present a similar pattern in either analysis. The component is characterised by the very high loadings on earlywood tracheid lumen width (+0.91, +0.87) and cell diameter (+0.94, +0.85). Latewood tracheid diameter has its highest loading on z_2, but the correlation (+0.57, +0.52) is relatively weak. The latewood ratio has a low to moderate (-0.21, -0.51) affinity with z_2. Of the remaining densitometric features ring minimum density alone has a low to moderate

affinity with z_2 (-0.22, -0.45): The correlation of the component with each of the other densitometric variables is weak or negligible.

The second component represents a major aspect of the variation among the wood character measures associated with the widths of the cells, particularly the earlywood tracheids (and lumen widths, which largely determine the overall C.S. diameter of the earlywood tracheids — see zero-order correlation (+0.98, +0.97) — Table 4.3 B,C). This variation is largely independent (in a statistical sense) of the variation of the densitometric characteristics other than the latewood ratio, and, to a limited extent, ring minimum density. By inference, the width of the wood cells, although representing a large element of the overall variation in the wood, have little influence upon its densitometric features.

The third component, z_3, accounts for 10% and 12% of the variance of the respective correlation matrices $\underline{R}^B$ and $\underline{R}^C$. The pattern of variable loadings on z_3 is generally similar in either analysis, but the relative magnitude of the loadings of the variables most closely associated with the component differs. z_3 is characterised by the high loadings on latewood ratio (+0.73) and latewood width (+0.73) respectively in the analyses of variable sets B and C. In each case the correlation of z_3 with latewood width, latewood ratio, and latewood tracheid diameter is relatively high. There is a moderate loading of z_3 on ring width (+0.50) in the PCA of variable set B.

The component represents an element of variation in the latewood characteristics that is largely independent (in the statistical sense) of the variation of the absolute values of the densitometric characteristics of the wood and of the earlywood anatomy. The variation is expressed as a positive association of the latewood tracheid C.S. size and indices of intra-incremental latewood distribution and extent.

The first three components account for over 75% of the variance in each standardised data matrix ($\underline{R}^B$, $\underline{R}^C$).

The overall similarity of the fourth component, z_4, in either analysis is again evidenced by the relative magnitude of the factor loadings, although the signs (which are arbitrarily defined with respect to a particular component) are opposite. z_4 accounts for 8% and 7% of the variance of the respective correlation matrices $\underline{R}^B$ and $\underline{R}^C$. None of

factor loadings on z_4 are high, and the component is difficult to interpret.

The fifth component, z_5, accounts for 6% and 5% of the variance of $\underline{R}^B$ and $\underline{R}^C$ respectively. The components in either analysis are essentially similar, although the loadings are of opposite (arbitrary) sign. The component is characterised by a moderately high loading of latewood ratio (0.52, 0.53). There is a consistent correlation of z_5 with the contrast between latewood ratio and earlywood tracheid wall thickness. The small variance of this contrast suggests that it represents a constant balance rather than a variable function.

Groupings of variables that have similar affinities with the principal axes of variation of the variable sets B and C are discernible on the scatter diagrams of the first 4 principal components plotted against one another (Figures 4.3 b,c). The groupings on each component pair comprise variables whose co-response with the main gradients of simultaneous variation among the wood characters is similar.

Three effective dimensions of variation in the measured densitometric and anatomical features of the wood have been demonstrated. The major component of variation accounts for nearly 50% of the variance of the standardised measures. It is highly correlated with each of the variables' ring mean density, ring maximum density, and latewood percentage; any of which could determine the component. Earlywood tracheid lumen width or earlywood tracheid diameter can effectively determine the second component, which accounts for almost 20% of the variation. The third component could be determined by either the intra-incremental latewood width or the latewood ratio.

The measure of one of these important variables from each of the three components would be required to effectively describe the variation of the densitometric and anatomical characteristics of the wood. Ring mean density alone effectively describes almost 50% of the variation.

4.3 THE SYSTEMATIC VARIATION OF SOME WOOD CHARACTERS WITHIN THE STEM

Within the stem the patterns of variation of wood characters is multidimensional and may be complex. Specific wood characters respond, to a varying extent, to the influence of factors, e.g., proximity to the sources of photosynthate or growth regulatory substances, which may vary more or less regularly as the tree ages. As a consequence, an element of the variation of the wood characters is systematic in nature.

This variation may be analysed in a series of simple two-dimensional sequences. The objectives of the analysis will determine the type of positional sequence used: Series effectively related to the pattern of growth of the tree are appropriate to a biologically-oriented analysis; other positional series may yield information of industrial application.

Growth-oriented sequences have been discussed in detail by Duff and Nolan [1953]. Wood characters may be examined in relation to their distribution along three positional series: (i) An oblique series within a given growth sheath down the stem from apex to base. (ii) A horizontal series from the pith outwards at a given height. Growth rings outward from the pith have been laid down by a cambium of increasing age. (iii) A vertical series at a given number of growth rings from the pith at different internodes from the stem apex. The annual rings, uniformly located with respect to pith, represent tissue developed by a uniform age cambium.

The system of sampling used in this study (see discussion in Chapter 2) was designed to facilitate an examination of systematic patterns of variation of wood characteristics in relation to the growth characteristics of the trees.

4.3.1 WOOD DENSITY

4.3.11 The Variation of Wood Density Features Outward from the Pith

A Review of Literature

There is general agreement among the authors of comprehensive literature reviews (Spurr, Hsiung, 1954; Larson, 1957; Goggans, 1961; Tappi, 1962; Paul, 1963; Elliot, 1970) that there is an increase in whole-ring wood density with increasing age from the pith in plantation-grown conifers. In some instances wood density, after increasing for a period of time, levels off and then fluctuates to the bark. This trend was observed in 15 to 30-year old plantation-grown slash pine (*P. elliottii*) from Queensland [Dadswell, Nicholls, 1959], where density increased in successive growth rings from the pith towards the bark but appeared to be more or less constant after the fifteenth ring. In some instances there is a decrease in wood density outward from the pith in the so-called senescent wood [Dadswell, 1958] of the outer rings of "over-mature" trees.

There are few published reports of radial variation of wood density in tropical pine species for trees of sufficient age to have produced adult wood (as cf. corewood). In trees of *Pinus kesiya* from Zambia exhibiting 24 growth rings at 5 feet above ground, a marked systematic increase of wood density from the pith outwards appeared to have stabilised at a roughly constant density value by the twentieth ring [Burley, Andrews, 1970; Burley, 1970].

Mean density increased with ring number, but at a declining rate, in 3 trees of *Pinus merkusii* grown in Zambia [Andrews, Burley, 1973]. Schmidt and Smith [1961] were unable to find any statistically significant trends of radial variation of ring mean density with age or distance from the pith in basal samples from 5 26-year old stems of *Pinus caribaea* (presumed to be of Cuban seed origin; i.e., *P. caribaea* var, *caribaea*) from a plantation in northern New South Wales. Lantican [1972] demonstrated a quadratic trend of increase of whole-ring wood density

(unextracted) with increasing age from the pith at each of 4 height levels (10% - 60%) in ten 30-year old trees of *Pinus caribaea* from a natural stand at Mt. Pine Ridge, British Honduras. Density increased rapidly with age from the pith until ring 11 - 14 and increased very much more gradually with further increase in age.

Two zones of wood about the pith of a mature conifer stem are now commonly recognised: The corewood or juvenile zone, and the adult-wood zone [Zobel, McElwee, 1958; Zobel, Ralston, Roberds, 1965; Elliott, 1970]. The zones are not precisely defined, but they represent essentially different physiological environments of wood formation.

The corewood zone, centred on the pith, extends from base to apex of the tree and is reported [see review of Elliott, 1970] as being between 5 and 15 annual rings in extent. It is related to age rather than to linear distance from the pith [Paul, 1960; Polge, 1964; Zobel, Webb, Henson, 1959]. The characteristics of the corewood have been described variously in terms of progressive changes of the anatomy, structure, and properties of the wood with increasing age from the pith. The proximity of the corewood to the pith and thus to the immediate vicinity of the live crown at the time of wood formation, and the progressive changes in wood structure and properties with increasing age from the pith suggest that the corewood characteristics reflect the physiological activity of the tree at the site of wood formation. The response of wood formation to the physiological influences of the active regions of the live crown are discussed in detail by Larson [1969].

The radial variation of wood density within the corewood zone has been studied most extensively in temperate species of conifers. There are conflicting reports of an initial increase or decrease in ring mean density outward from the pith [Elliott, 1970]. The evidence available from studies in which annual ring structure is considered [e.g., Taras, 1965; Brazier, 1967; Dadswell, Nicholls, 1959] shows that, for those species that show a clearly defined latewood zone, earlywood density values progressively decrease from the pith, and latewood density values increase from the pith, over a period comparable with corewood formation. Much of the variation of mean density values within the corewood can therefore be attributed to the balance between the

respective density values and the proportion of the earlywood and latewood tissue in the annual ring. Patterns of radial variation generally similar to those mentioned for earlywood and latewood density have been reported for (earlywood) minimum and (latewood) maximum density values in studies using radiation techniques [Brazier, 1967; Harris, Polge, 1967; Phillips, 1960; Harris, 1972]. Harris [1969, 1973b] notes the following features of the variation of ring maximum and minimum density values (determined from radiological measures) that are common to most pines:

(1) Maximum (latewood) density values increase more or less abruptly from the pith outwards but soon tend to settle at some value that remains nearly constant from the corewood outwards. Values for maximum density usually show much greater variability between adjacent growth layers than do the corresponding values for minimum density.

(2) Minimum (earlywood) density values usually decrease over the first two to four growth layers from the pith but thereafter remain constant or may slowly increase and settle at some value which remains fairly constant outside the corewood.

Because the wood of the corewood zone is associated with properties, e.g., high longitudinal shrinkage and low density values, that are undesirable for many end uses, its importance to utilisation practice increases as the rotation age decreases. Zobel *et al.* [1965] demonstrated a strong ($r = -0.84$) negative correlation of stand age and percentage corewood in loblolly pine plantations; e.g., a 48-year old stand and an 18-year old stand growing on similar sites had 8, and 47 per cent corewood respectively, indicating that with rotations 20 years or less corewood will constitute a major portion of the volume utilised. The elucidation of the variation of the wood characteristics of this zone is of special importance in a species such as *Pinus caribaea* which is grown in tropical and subtropical areas where proposed rotations are, by comparison with temperate regions, very short; with the result that the properties of the corewood will play a decisive role in determining the quality of the end product.

There are few published reports of wood density features of the corewood region of tropical coniferous species, in which the sampling

schedule is sufficiently intensive to allow a detailed assessment of the radial patterns of variation. The radial variation of wood mean density in 10-year old *Pinus caribaea* var. *hondurensis* from Jamaica [Brown, 1973; Burley, Hughes, Franklin, Gourlay, 1973] was assessed from samples taken at fixed percentages of radial distance from pith to bark. A general linear increase of density with distance from the pith [Brown, 1973], and a slight initial decrease (between 10% and 30% of radial distance from the pith) followed by a linear increase [Burley *et al.*, 1973] were noted.

The radial variation of maximum, minimum, and mean density in successive annual growth increments from the pith to the twelfth ring was determined from breast height samples of *P. caribaea* var. *hondurensis*, *P. merkusii*, and *P. oocarpa* (6 rings) grown in West Malaysia, using the beta-ray technique [Harris, 1973a]. All three species were characterised by a central core (extending to the second or fourth growth layers from the pith) of low density wood containing poorly developed latewood. Very dense latewood (extractive-free ring maximum density values 0.8 - 1.0 gm/cm^3 at 10% moisture content), commonly occurring as numerous "false rings" within each annual growth layer, was formed outside the central core. The rapid change from corewood to outer wood resulted in very steep density gradients from the pith outwards, but this trend appeared to terminate by the twelfth growth layer. It was concluded, on this evidence, that corewood formation is complete by the twelfth growth layer from the pith, and that a fairly uniform level of wood density could be expected to be maintained in subsequent growth rings.

Results and Discussion

The average ring values, derived from the pooled estimates of 20 trees, for the densitometric features (maximum, minimum, and mean density, latewood percentage, and ring width) of the wood of each annual growth increment, at 6 height levels, are presented in Tables 4.5 a - c.

The horizontal variation of each of these features at 20% of total tree height is depicted graphically in Figure 4.4. In Figure 4.5, the horizontal variation of the parameters (average ring values) of mean density, latewood percentage, and ring width for corresponding annual increments at breast height, 10%, 20%, 40%, 60%, and 80% of total tree height are shown.

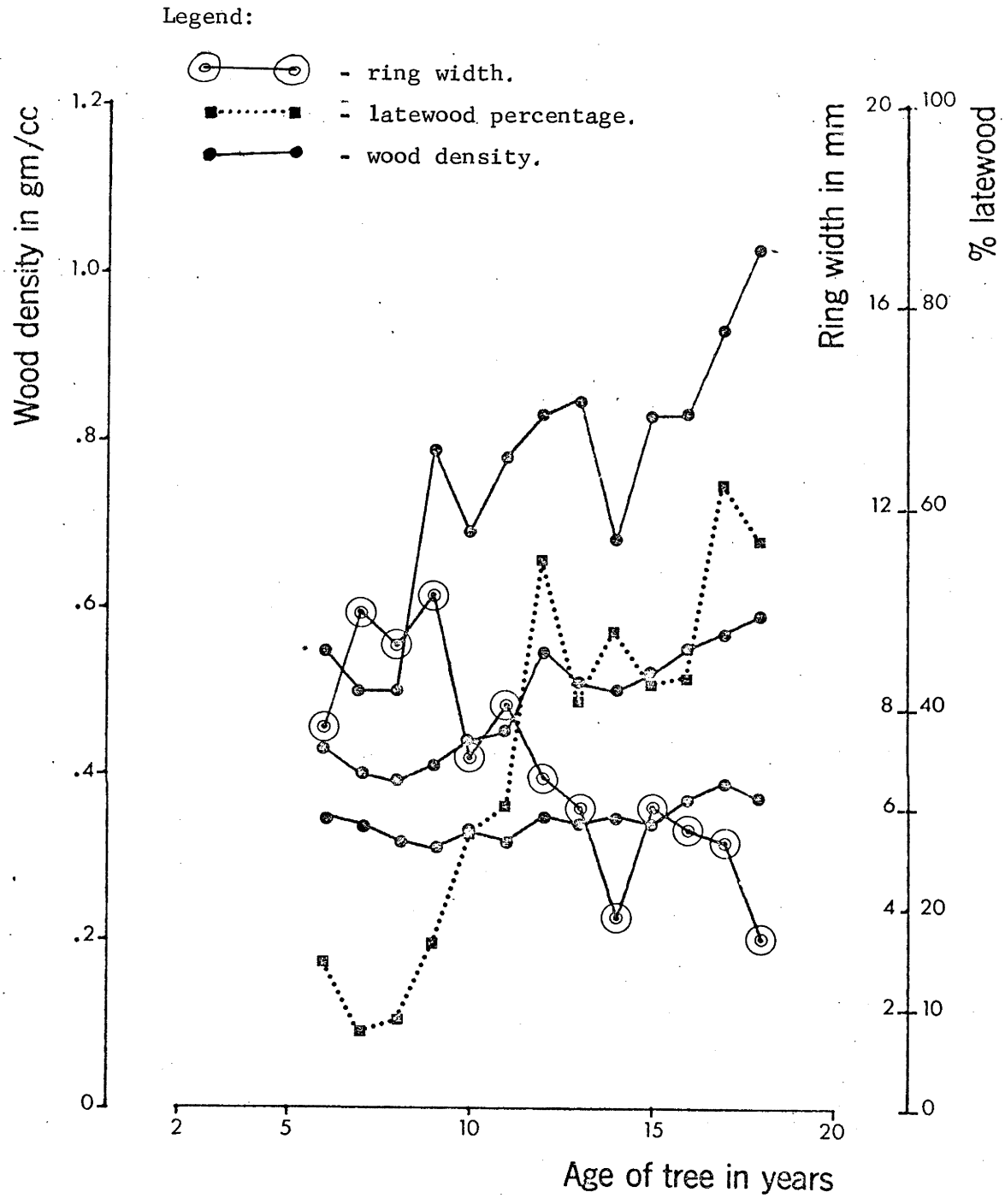
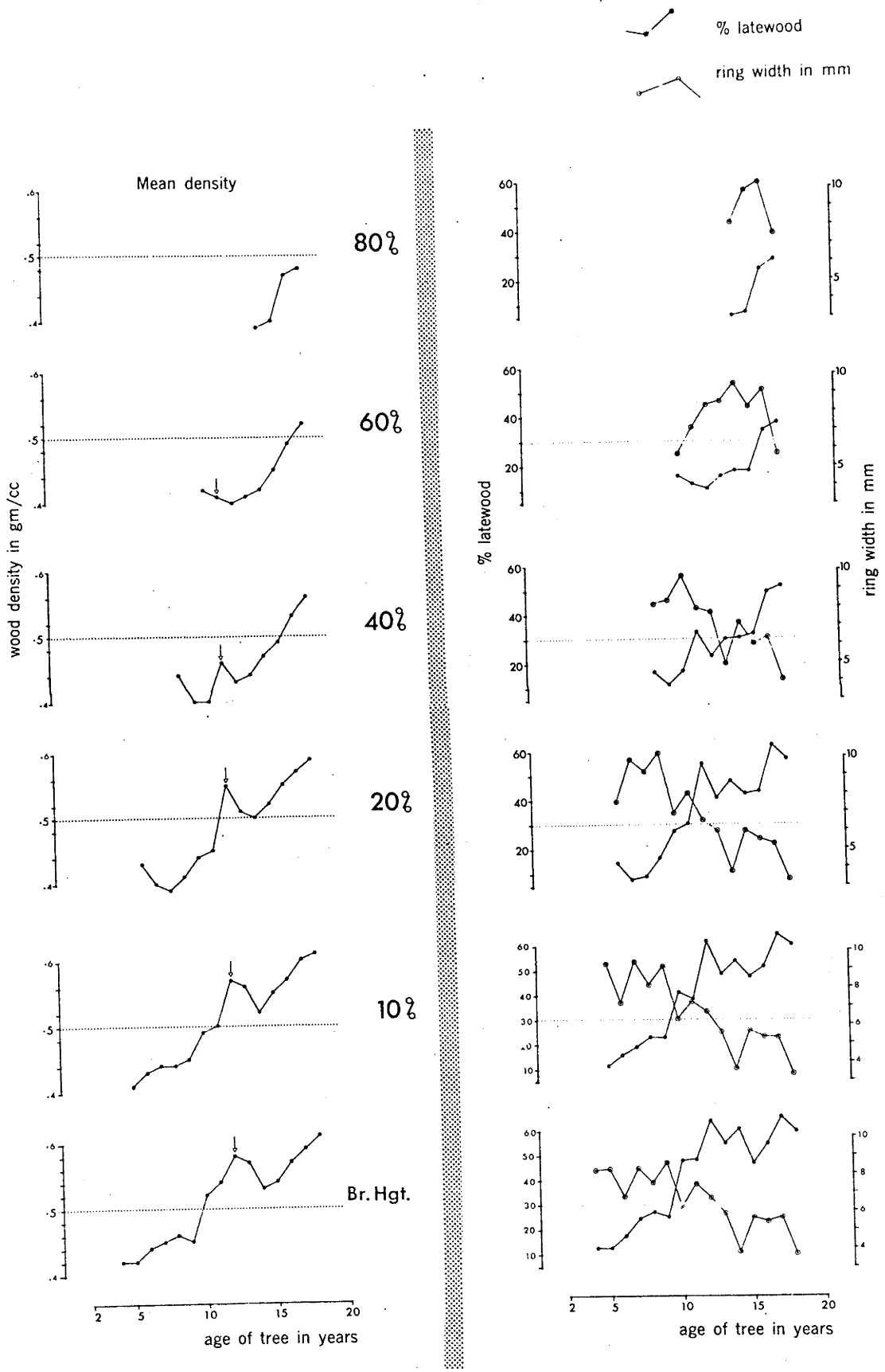


Figure 4.4: The horizontal variation of wood densitometric features (maximum, minimum, and mean density; latewood percentage; ring width) of successive annual growth increments at 20% of total tree height at the time of sampling. Each point on the curves represents the pooled data of the corresponding annual increments (measured from the bark) of 20 trees. Total tree age is measured from seedling transplant (1952): Growth rings are arranged with reference to the outermost ring, which corresponds with tree age 18 years.

Figure 4.5: The horizontal variation of mean density, latewood percentage, and ring width of successive annual growth rings at 6 height levels. Each point on the curves represents the pooled data of the corresponding annual increments (measured from the bark) of 20 trees. Percentile heights are percentage of total tree height at the time of sampling (December, 1970). Age of tree refers to the number of years since seedling transplantation (1952): The growth rings in each height level are arranged with reference to the outermost ring, which corresponds with a tree age of 18 years.


% latewood
ring width in mm
Mean density
80%
60%
40%
20%
10%
Br. Hgt.
wood density in gm/cc
% latewood
ring width in mm
age of tree in years
age of tree in years

Tables 4.5 a - e: Mean values and standard errors of the ring densitometric characters [(a) maximum density; (b) minimum density; (c) mean density; (d) latewood percentage; (e) ring width] for each annual increment at 6 height levels. Each value represents the pooled data of the 20 trees of subplots A and B for the corresponding annual increments (measured from the bark) at each of the height levels. Total tree age is measured from seedling transplant (1952). Percentile heights are percentage of total tree height at the time of sampling (December, 1970).

Table 4.5a: Ring maximum density.

Ring number (from bark)	Total age of tree (yrs)	Height in tree											
		Breast height (1.3 m)		10%		20%		40%		60%		80%	
		mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
1	18	1.09	.03	1.08	.04	1.03	.03	.99	.03	.94	.04	.84	.04
2	17	.95	.03	.97	.03	.93	.03	.89	.03	.84	.04	.71	.03
3	16	.90	.03	.88	.03	.83	.04	.77	.04	.66	.04	.50	.01
4	15	.85	.03	.85	.03	.83	.03	.76	.03	.68	.04	.47	.01
5	14	.69	.02	.71	.02	.68	.02	.63	.02	.59	.02		
6	13	.92	.03	.90	.03	.85	.04	.70	.04	.55	.03		
7	12	.86	.03	.88	.03	.83	.04	.68	.04	.51	.02		
8	11	.84	.03	.81	.04	.78	.04	.60	.03	.54	.03		
9	10	.80	.04	.78	.03	.69	.04	.52	.02				
10	9	.87	.03	.87	.03	.79	.04	.54	.02				
11	8	.69	.04	.66	.04	.50	.03						
12	7	.64	.03	.61	.03	.50	.01						
13	6	.67	.03	.66	.02	.55	.04						
14	5	.54	.02	.49	.02								
15	4	.52	.04										

The pattern of systematic variation of each of the densitometric features changes with height in the tree (Tables 4.5 a - e; Figure 4.5). Year by year fluctuations in the values of the parameters (pooled average values for corresponding annual rings of the 20 trees) are quite pronounced for maximum density, latewood percentage, and ring width, and of a moderate order for whole-ring mean density, but are relatively slight for minimum density.

(a). Ring Maximum Density

Ring maximum density is low (0.49 - 0.55) in the innermost rings (1 to 3 rings) at each height, but increases rapidly to very high values (0.80+); this steep gradient of increase in ring maximum density occurring over the inner 4 to 7 rings over the height range (Table 4.5a). Latewood is relatively poorly developed in the rings of this central core (ring values less than 30% — see Figure 4.5).

Within the central core there is a general linear increase in the values of both maximum density (Table 4.5a) and latewood percentage (Figure 4.5) outward from the pith in the lower bole (breast height to 10% of total tree height). The linear trend of increase of maximum density with increasing age of the growth increment (measured as the mean value for corresponding rings numbered from the pith as cf. corresponding annual increments — from bark) within the central core at breast height is shown in Figure 4.6a and Table 4.6. In the central stem (20% to 60% of total height) there is an initial decrease in maximum density and latewood percentage (over 2 to 3 rings) followed by a linear increase. An overall linear increase of maximum density and latewood percentage outward from the pith is again apparent in the upper stem (80% of total tree height).

The systematic radial trends of variation are well defined, and the year by year fluctuations of both maximum density and latewood percentage are of a relatively low order within the central core. Outwards from this zone (i.e., from about the eighth ring) there is a relatively gradual linear trend of increase of both maximum density and percentage latewood of the annual growth rings. There is no indication that the radial increase of either ring maximum density or latewood percentage has attained a maximum value, nor do the trends of increase show any sign of stabilising by the fifteenth (outermost) ring laid down at tree age 18 years.

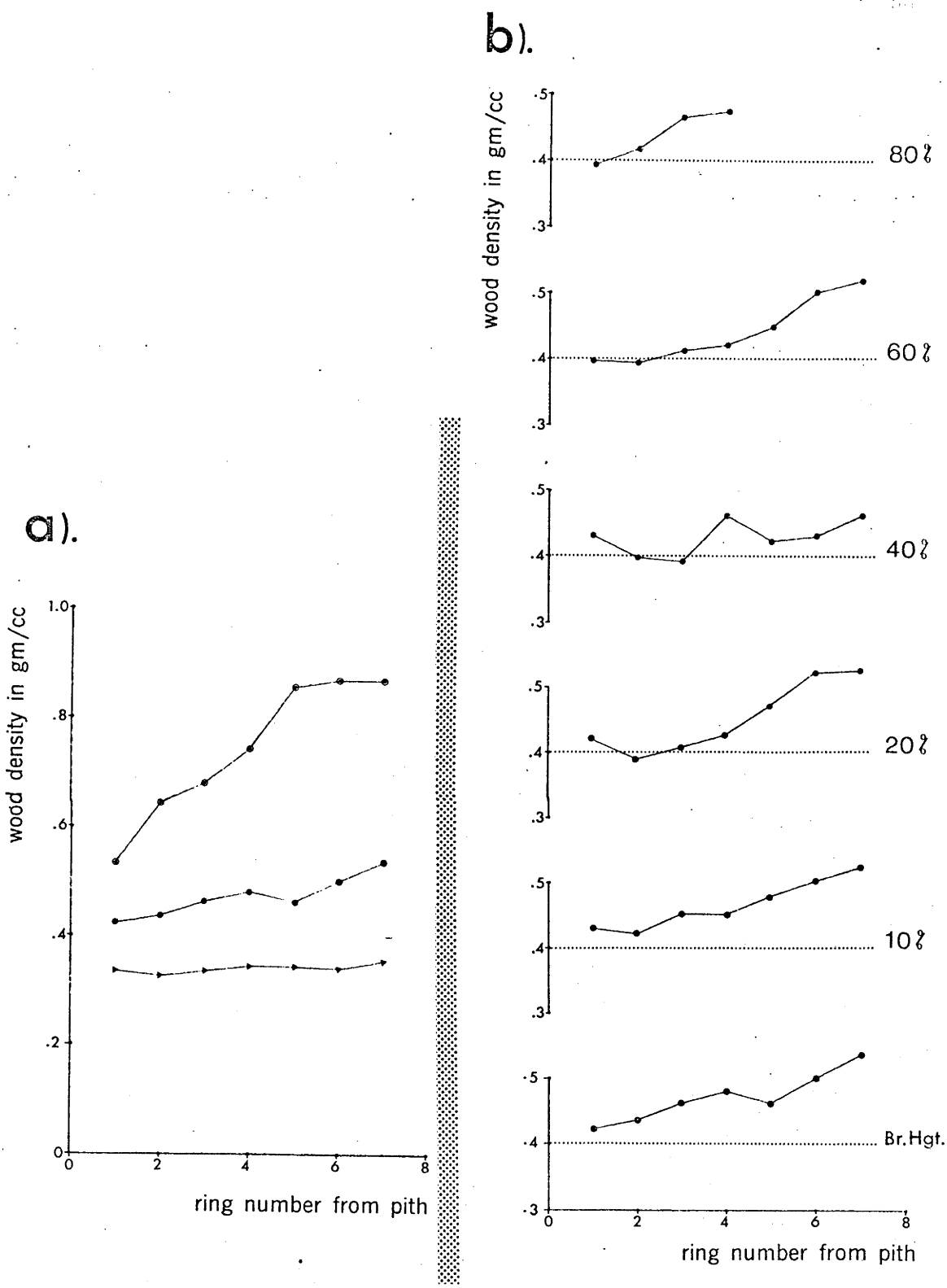


Figure 4.6: The horizontal variation of wood density with age of the annual growth increment (measured as ring number from the pith). Each point on the curves represents the pooled data of rings of the same age in the 10 trees of sub-plot A.

(a) The variation of ring maximum, minimum, and mean density with age at breast height (1.3 m).

(b) The variation of ring mean density with age at 6 height levels. Percentile heights are percentage of total tree height at the time of sampling (December, 1970).

Table 4.6: Mean values and standard deviations for the pooled data (10 trees of sub-plot A) of wood density (maximum, minimum, mean) of growth rings of corresponding age (measured as ring number from the pith) at breast height (1.3 m).

Ring No. (from pith)	Maximum density		Minimum density		Mean density	
	mean	s.d.	mean	s.d.	mean	s.d.
1	.533	.077	.335	.035	.423	.040
2	.644	.088	.326	.032	.437	.053
3	.680	.120	.335	.026	.463	.057
4	.744	.127	.344	.035	.481	.048
5	.858	.128	.343	.035	.463	.061
6	.871	.179	.340	.032	.501	.071
7	.871	.154	.354	.043	.537	.063

The year by year fluctuation of the values of maximum density and latewood percentage about the overall linear trend of increase are quite pronounced; considerably more so than the annual fluctuations within the inner core. This evidence suggests that the response of latewood characteristics during the period corresponding with "corewood" formation is determined to a greater degree by inherent patterns of change in the physiological environment of wood formation associated with proximity to the stem apex and terminal meristems of the lateral shoots and the source of photosynthate (i.e., "age" effects), and is less subject to environmental influence than is the response of latewood characteristics of the wood formed distally to the inner core, where the influence of the environment assumes greater significance.

(b). Ring Minimum Density

Both the range of systematic variation outwards from the pith and the variability between adjacent growth layers are very much less for ring minimum density than for the corresponding values of maximum density (Table 4.5b).

Over the innermost approximately 8 rings (i.e., the period corresponding with the formation of the inner core defined in the previous sub-section in terms of levels and gradients of maximum density and latewood) the systematic variation of ring minimum density outwards from the pith shows changes with height in the tree which parallel the changes in ring maximum density and latewood development. In the lower

Table 4.5b: Ring minimum density. (caption facing p.55).

Ring number (from bark)	Total age of tree (yrs)	Height in tree											
		Breast height (1.3 m)		10%		20%		40%		60%		80%	
		mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
1	18	.39	.01	.39	.02	.37	.01	.37	.01	.35	.01	.34	.01
2	17	.40	.01	.40	.01	.39	.01	.37	.01	.35	.01	.34	.01
3	16	.39	.01	.39	.01	.37	.01	.35	.01	.34	.01	.34	.01
4	15	.36	.01	.36	.01	.34	.01	.33	.01	.33	.01	.34	.01
5	14	.37	.01	.36	.01	.35	.01	.34	.01	.33	.01		
6	13	.37	.01	.36	.01	.34	.01	.33	.01	.33	.01		
7	12	.37	.01	.36	.01	.35	.01	.33	.01	.33	.01		
8	11	.35	.01	.34	.01	.32	.01	.31	.01	.34	.01		
9	10	.35	.01	.34	.01	.33	.01	.32	.01				
10	9	.34	.01	.33	.01	.31	.01	.35	.01				
11	8	.34	.01	.33	.01	.32	.01						
12	7	.34	.01	.33	.01	.34	.01						
13	6	.33	.01	.34	.01	.35	.01						
14	5	.33	.01	.33	.01								
15	4	.33	.01										

bole (i.e., from breast height to 10% of total tree height) there is a very gradual linear increase (0.33 - 0.34) in the value of minimum density of successive annual increments (Table 4.5b). In the central stem (20% to 60% of total height) there is a negative quadratic trend of variation of ring minimum density outward from the pith; the value decreasing (0.35 - 0.31) over the first 2 to 4 growth layers from the pith and then gradually increasing (Table 4.5b). This is a trend commonly encountered in temperate pine species [Harris, 1973b]. A trend of linear constancy (0.34) of minimum density outward from the pith is evident at 80% of tree height.

Distal to the central core there is a linear trend of gradual increase of ring minimum density outward from the pith which shows no evidence of having reached a maximum level or of stabilising by the fifteenth ring.

(c). Ring Mean Density

The value of whole-ring mean density is relatively low (< 0.50) in the inner 6 to 8 rings, i.e., over the period corresponding with "corewood" formation (Table 4.5c; Figure 4.5). The pattern of variation of mean density outward from the pith within this zone changes with height in the tree; the general trends paralleling those of ring maximum and minimum density (Tables 4.5 a,b,c; Figures 4.4, 4.5). In the lower stem (breast height to 10% of tree height) there is a general linear trend of increase. In the central part of the stem (20% to 60% of tree height) there is a decrease in the value of mean density over the first 2 or 3 rings followed by a general trend of linear increase. The gradient of linear increase of mean density outward from the pith in the innermost rings is greatest in the upper stem (80% of tree height).

Distal to the central "core" there is a linear trend of increase of ring mean density outward from the pith, with no evidence of the trend stabilising by the fifteenth ring. The systematic trend of radial variation is quite pronounced, but there are moderate year by year fluctuations which are consistent between heights, and which presumably reflect the response of whole-ring mean density to the influence of environmental change.

Conjectures about the response of variation in whole-ring density values in relation to physiological influence are complicated

Table 4.5c: Ring mean density. (caption facing p.55).

Ring number (from bark)	Total age of tree (yrs)	Height in tree											
		Breast height (1.3 m)		10%		20%		40%		60%		80%	
		mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
1	18	.61	.01	.61	.02	.59	.01	.56	.01	.52	.01	.48	.01
2	17	.59	.01	.60	.02	.57	.01	.53	.01	.49	.01	.47	.01
3	16	.57	.01	.57	.01	.55	.02	.49	.02	.45	.02	.40	.01
4	15	.54	.01	.55	.01	.52	.01	.47	.02	.42	.01	.39	.01
5	14	.53	.01	.52	.01	.50	.01	.44	.01	.41	.01		
6	13	.57	.01	.56	.02	.51	.02	.43	.02	.40	.01		
7	12	.58	.01	.57	.01	.55	.02	.46	.02	.41	.02		
8	11	.54	.01	.50	.02	.45	.02	.40	.02	.42	.02		
9	10	.52	.01	.49	.01	.44	.02	.40	.01				
10	9	.45	.01	.45	.01	.41	.01	.44	.01				
11	8	.46	.01	.44	.02	.39	.01						
12	7	.45	.01	.44	.01	.40	.01						
13	6	.44	.01	.43	.01	.43	.02						
14	5	.42	.01	.41	.01								
15	4	.42	.02										

because whole-ring mean density values are a complex function of the density of both earlywood and latewood tissues and also of the relative amounts of the respective tissues produced in the annual increment. Density values vary considerably within either of these zones [see Harris, 1969], and the specific environmental conditions that influence the density values in either zone could presumably be independent of one another in quality as well as in time.

In this regard, the most pronounced indications of environmental influence in the mean density curves (Figure 4.5), viz., the consistently high values in ring 7 (from bark) and the depressed values in ring 5, are of interest. In ring 7 the proportion of latewood is unusually high (see latewood percentage values of Figure 4.5), whereas the ring width (Figure 4.5) and maximum density (Table 4.5a) are consistent with expected "normal" values for wood of that age. The high value of mean density is largely a response to the relative proportion of latewood to earlywood tissue in the ring. In ring 5, by contrast, the latewood percentage is moderate and ring width (growth rate) is low but the density of the latewood (maximum density value — Table 4.5a) is consistently low and this factor appears to exert the dominant influence on the depressed value of whole-ring mean density.

The environmental factors that induced the high values of latewood percentage and of mean density in ring 7 (from bark) had their greatest influence in wood formed distal to the inner core, and their influence upon the values of these characters in wood formed close to the pith (and thus in the upper regions of the live crown — see 60% height level in Figure 4.5) was negligible. This evidence suggests that (as with maximum density — see previous sub-section) the effect of environmental influence upon these wood characteristics is most highly pronounced in wood formed outside the physiologically active region of the live crown, and that, within the active live crown, developmental effects associated with age (and consequently proximity to the stem apex and terminal meristems of the lateral shoots) are of prime significance.

(d). Latewood Percentage

The variation of latewood development outward from the pith was discussed in relation to the concomitant variation of maximum (latewood) density. The mean values and their standard errors corresponding with the parameters depicted graphically in Figure 4.5 are presented in Table 4.5d.

Table 4.5d: Latewood percentage. (caption facing p.55).

Ring number (from bark)	Total age of tree (yrs)	Height in tree											
		Breast height (1.3 m)		10%		20%		40%		60%		80%	
		mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
1	18	60.1	3.94	60.5	4.67	56.7	3.80	51.4	4.07	37.7	3.38	28.2	2.60
2	17	65.8	4.47	64.6	5.30	62.4	4.36	49.0	5.27	34.4	4.77	24.4	3.27
3	16	55.1	3.78	51.4	5.24	43.4	4.41	31.8	4.10	18.1	3.20	6.81	1.58
4	15	47.0	3.15	47.5	3.22	42.4	2.80	30.3	3.08	18.1	2.60	5.51	3.10
5	14	60.9	3.32	53.8	4.22	47.8	4.59	29.9	4.26	15.8	4.08		
6	13	55.2	3.72	48.5	3.85	40.8	3.92	22.9	3.89	11.0	2.70		
7	12	64.3	3.30	61.7	3.71	54.8	4.56	32.9	4.85	12.9	3.73		
8	11	48.5	3.43	38.5	3.74	30.3	3.57	16.9	3.39	16.2	4.19		
9	10	48.1	4.43	41.2	4.21	27.4	5.01	11.2	2.68				
10	9	25.4	2.88	22.9	2.63	16.5	2.37	16.5	3.18				
11	8	27.2	3.79	23.1	3.84	8.9	2.44						
12	7	24.5	3.92	19.0	3.22	7.7	2.28						
13	6	17.6	2.11	15.7	2.44	14.4	6.37						
14	5	12.7	2.63	11.3	3.97								
15	4	12.8	5.62										

Within individual trees latewood is generally poorly developed or even absent altogether between one and four growth layers from the pith. Thereafter (varying from the second to the fifth growth layer) latewood is well developed. In most growth increments there is a single distinct major zone of latewood formation, but the occurrence of several narrow bands of latewood (what would be described as "false rings" in temperate zone conifers) separated by wood of low density within an annual increment is not uncommon. The pattern of "false ring" development is consistent between corresponding annual increments (counted from the outer ring) over the height range within trees, and a generally similar pattern is evident between trees.

The within-tree pattern of latewood development is shown in the densitometric tracings (Figure 4.7) of tree A.1 (a vigorous co-dominant – see Figures 4.16 - 18). The poor development of latewood, with low values of maximum density in the innermost 3 rings, and the very rapid gradient of increase of maximum density outwards to roughly the seventh or eighth growth ring from the pith are evident from these tracings.

(e). Ring Width

The pattern of variation of ring width outward from the pith changes considerably with height (Figure 4.5; Table 4.5e). In the lower stem (breast height to 10% of total tree height) ring width fluctuates about a relatively high value (6.8 - 9.4 mm) in the innermost 5 or 6 rings: Outwards from this region there is a linear trend of decrease in ring width. Higher in the stem ring width tends to increase initally; the tendency being most highly pronounced at 60% of total tree height.

Relatively high values of ring width (generally in excess of 6 mm for pooled tree means) are encountered in the inner "core" of 7 or growth increments.

The pattern of variation of the width of corresponding annual increments (counted from bark) is quite similar from breast height to 40% of tree height. This is so both for the systematic decrease outward from the pith associated with age, and the fluctuations in adjacent growth layers that reflect response to changes in the environment. In the upper stem (60% to 80% of total tree height) the pattern of variation of ring width outward from the pith differs considerably from the variation over corresponding annual increments in the lower stem.

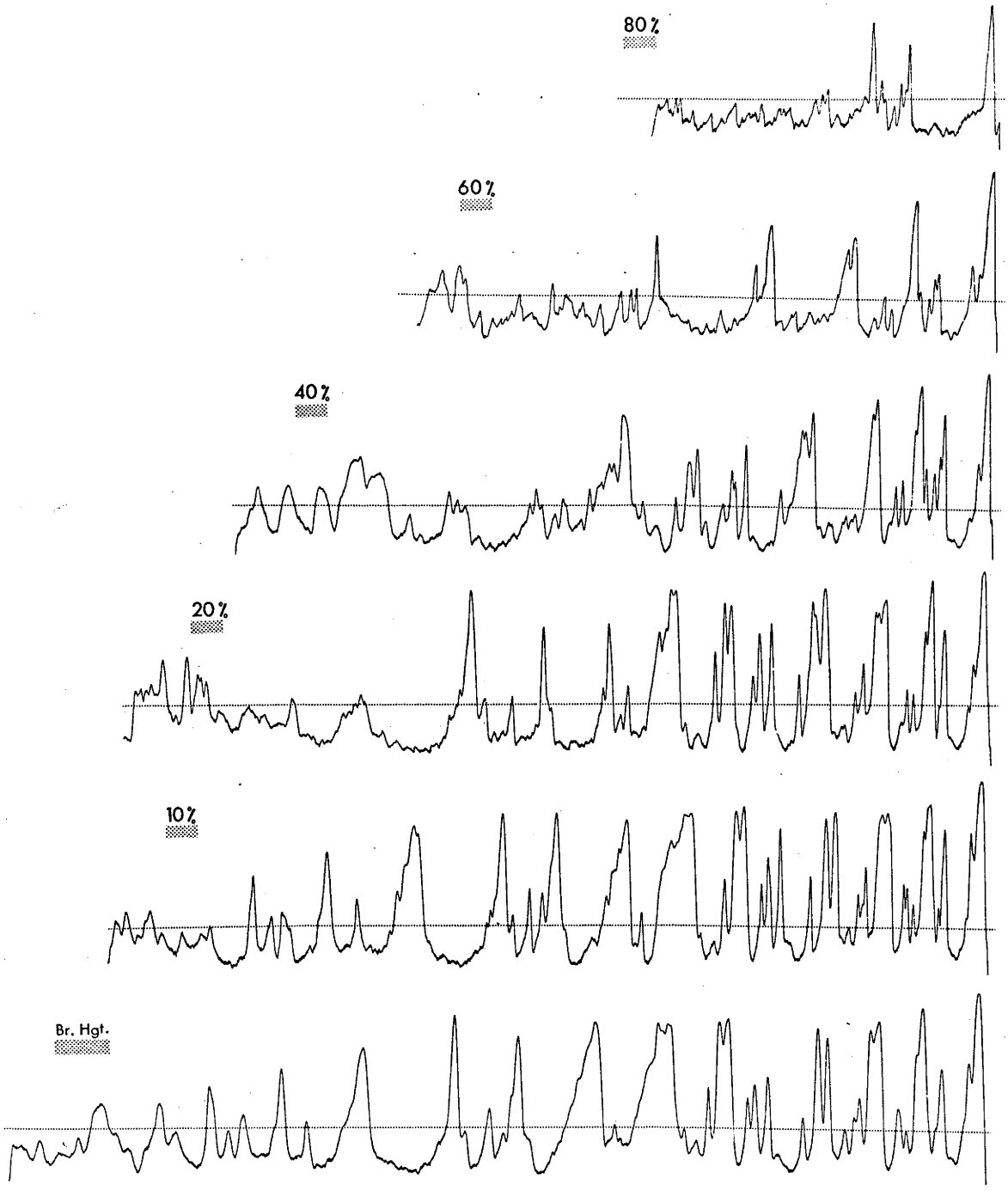


Figure 4.7: Densitometric tracings which approximate the variation of wood density from the pith to the outermost growth increment (left to right in the figure) at 6 height levels in tree A.1 (a vigorous co-dominant).

The dotted line represents a wood density of 0.468 g/cc; an arbitrary value which is used to delimit "earlywood" and "latewood".

Percentile heights are percentage of total tree height at the time of sampling.

Table 4.5e: Ring width. (caption facing p.55).

Ring number (from bark)	Total age of tree (yrs)	Height in tree											
		Breast height (1.3 m)		10%		20%		40%		60%		80%	
		mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
1	18	3.67	.38	3.36	.31	3.37	.34	4.08	.43	5.71	.55	7.52	.56
2	17	5.66	.59	5.32	.53	5.28	.50	6.37	.68	9.15	.96	10.27	.56
3	16	5.42	.50	5.35	.48	5.54	.49	6.02	.53	8.24	.70	9.82	.60
4	15	5.64	.41	5.69	.39	6.01	.40	7.20	.52	9.50	.69	8.10	.71
5	14	3.79	.25	3.65	.20	3.79	.22	4.94	.40	8.54	.92		
6	13	5.85	.49	5.62	.49	5.99	.48	7.76	.62	8.33	.89		
7	12	6.72	.53	6.73	.51	6.60	.50	7.99	.57	7.11	.68		
8	11	7.47	.57	7.27	.55	8.06	.59	9.76	.69	5.69	.81		
9	10	6.21	.40	6.35	.35	6.99	.44	8.43	.41				
10	9	8.61	.49	9.18	.52	10.26	.60	8.23	.65				
11	8	7.51	.41	8.19	.48	9.25	.52						
12	7	8.30	.53	9.44	.53	9.91	.46						
13	6	6.77	.38	7.22	.44	7.60	1.18						
14	5	8.26	.57	9.34	.78								
15	4	8.20	.65										

4.3.12 The Variation of Wood Density with Height in the Tree

12.1 The Variation of Density of the Stem Cross-Section with Height

In species of the genus Pinus the density of wood over an entire cross-section has, in general, been shown to decrease with increasing height in the stem (Spurr, Hsiung, 1954; Larson, 1957; Okkonen, Wahlgren, Maeglin, 1972). This pattern has been observed in var. hondurensis (Brown, 1969, 1973; Burley et al., 1973; Lantican, 1972).

The weighted average disc values of the ring mean, maximum, and minimum density for the five levels from 10% to 80% of total height in each of the 20 trees are presented in Figure 4.8. The weighted average values for each of 7 densitometric characters (ring maximum, minimum, and mean density, density range, latewood percentage, width of the intraincremental latewood zone, and latewood ratio) at each height level in individual trees are presented in Appendix 4. The system of weighting is described in Section 4.4.

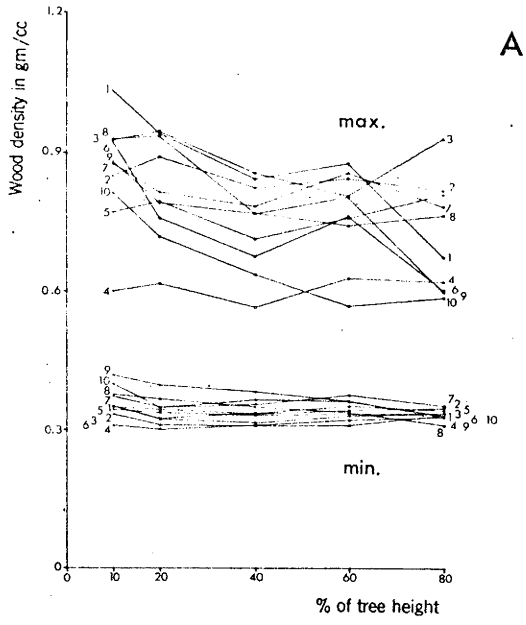
The average pooled estimates for all trees are shown in Figure 4.8. Errors associated with these estimates, and the equivalent arithmetic values are presented in Tables 4.12 a - c. The weighted averages are more meaningful than arithmetic estimates, particularly if population mean values are considered.

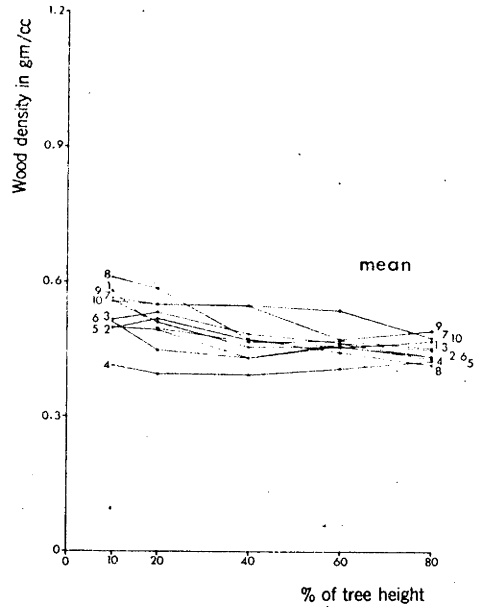
(a). Ring Minimum Density

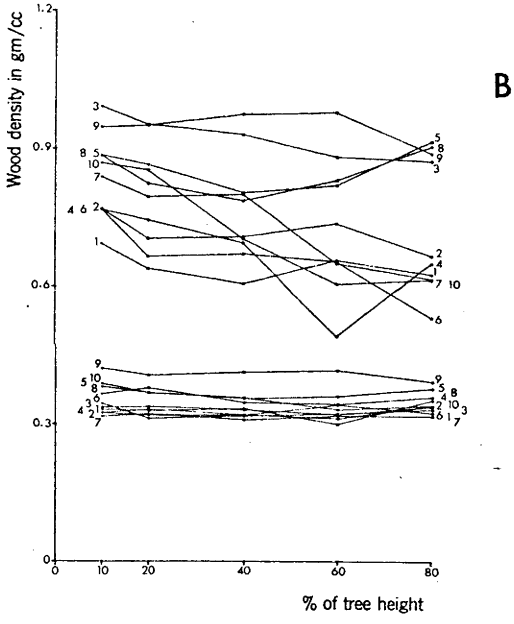
There is only slight variation with height of the weighted disc average value of minimum density within trees, and the trend, both within trees and for the pooled mean estimate, is essentially linear (Figure 4.8). In the majority of trees the minimum density remains constant with height. There is a systematic decrease of minimum density with height in 3 trees (A.8, 9, 10) which have higher than average minimum density values in the lower stem, but the trend of constancy of minimum density with height prevails in other trees with high (e.g. B.5, 8, 9) or low values.

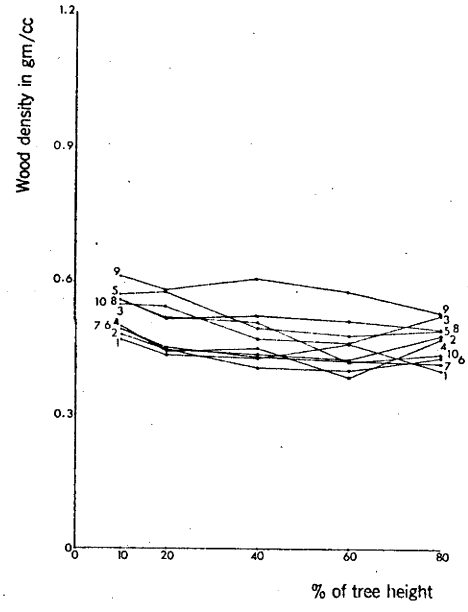
Figure 4.8: The variation with height of the weighted average disc values of ring maximum, minimum, and mean density in each of 20 trees (A.1 - 10; B.1 - 10) - upper figure.

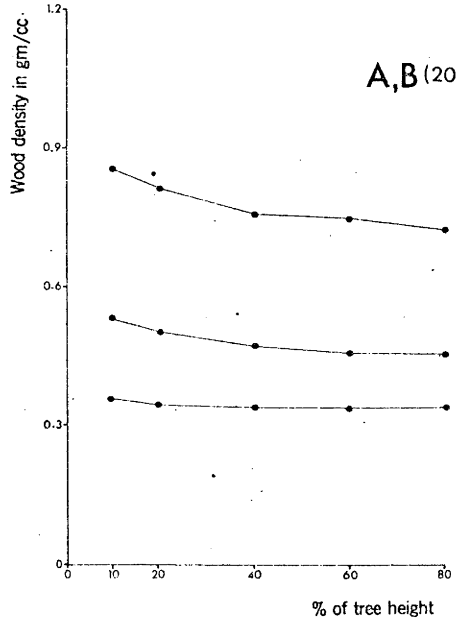
The average estimates from the pooled data of the 20 trees are shown in the lower figure.


A
max.
min.
Wood density in gm/cc
% of tree height


mean
Wood density in gm/cc
% of tree height


B
Wood density in gm/cc
% of tree height


Wood density in gm/cc
% of tree height


A,B (20 trees)
Wood density in gm/cc
% of tree height

(b). Ring Mean Density

Phenotypic differences between trees in the patterns of variation of the weighted disc average values of mean density are more diverse. No constant systematic trend between trees associated with differences in the absolute values of mean density is apparent; e.g., trees with high values in the lower stem may show either a marked systematic decrease in mean density with height (A.8), or an essentially constant value of mean density with height (B.9). The range of variation within trees and between trees is greater than for minimum density. The pooled mean estimate shows a systematic linear decrease with height. A linear decrease of average density with height (10% - 60%) was observed in 30-year old trees of *P. caribaea* from a natural stand at Mt. Pine Ridge, British Honduras [Lantican, 1972].

(c). Ring Maximum Density

The patterns of variation of the disc weighted average value of maximum density are highly variable between trees. They include trends of linear constancy (B.1), decrease (A.10, B.3, 10) or increase (A.4) with height, quadratic trends where maximum density decreases (B.5, 8) (increases — B.9) with height to a minimum (maximum) and then increases (decreases), and other less regular trends. There are marked phenotypic differences between trees in the within-tree range of maximum density. No constant systematic trend between trees associated with differences in the absolute value of maximum density is apparent. Phenotypic differences between trees in the absolute value of this character are of a high order. The pooled mean estimate of the disc weighted average values of maximum density shows a linear decrease with height (Figure 4.8). The decrease with height is considerably more pronounced for the pooled estimate of the disc arithmetic values (see Table 4.12A).

The variation of density of the stem cross-section in relation to height is affected by the reduction in the number of rings available for sampling with increase in height. Results quoted for variation of density with height are particularly sensitive to the distribution of samples within the stem [Wellwood, Jurazs, 1968].

2.2. The Variation of Wood Density with Height Within an Annual Growth Sheath

The variation, in relation to percentage of total tree height, of mean, maximum and minimum density within the third growth sheath from the bark, in each of the 20 trees, is shown in Figure 4.9. The pooled estimates of all trees are presented in Table 4.7.

Table 4.7: Mean values (20 trees) and standard deviations of maximum, mean, and minimum density at six height levels within growth sheath 3 (from bark). Growth sheath 3 was laid down at total tree age 16 years (1968). Percentile heights refer to percentage of total tree height at the time of sampling (age 18 years).

Height in tree	Maximum density		Mean density		Minimum density	
	mean	s.d.	mean	s.d.	mean	s.d.
Breast height	0.90	.122	.574	.048	.389	.030
10%	.878	.141	.570	.065	.386	.041
20%	.831	.164	.546	.085	.370	.040
40%	.768	.185	.490	.074	.355	.036
60%	.664	.178	.449	.071	.344	.030
80%	.497	.053	.402	.033	.342	.029

(a). Minimum Density

There is considerable variation between trees both in the absolute value of minimum density at a given level and in the pattern of variation of minimum density with height. Trends of variation with height are diverse, and include, for example, a pronounced decrease in minimum density (e.g. trees A.10, B.10), linear constancy (A.4) or gradual decrease (A.7, B.6, 7) with height, a negative parabolic trend (A.5), and other, less regular trends. In some trees (e.g. A.3, B.4, 8)

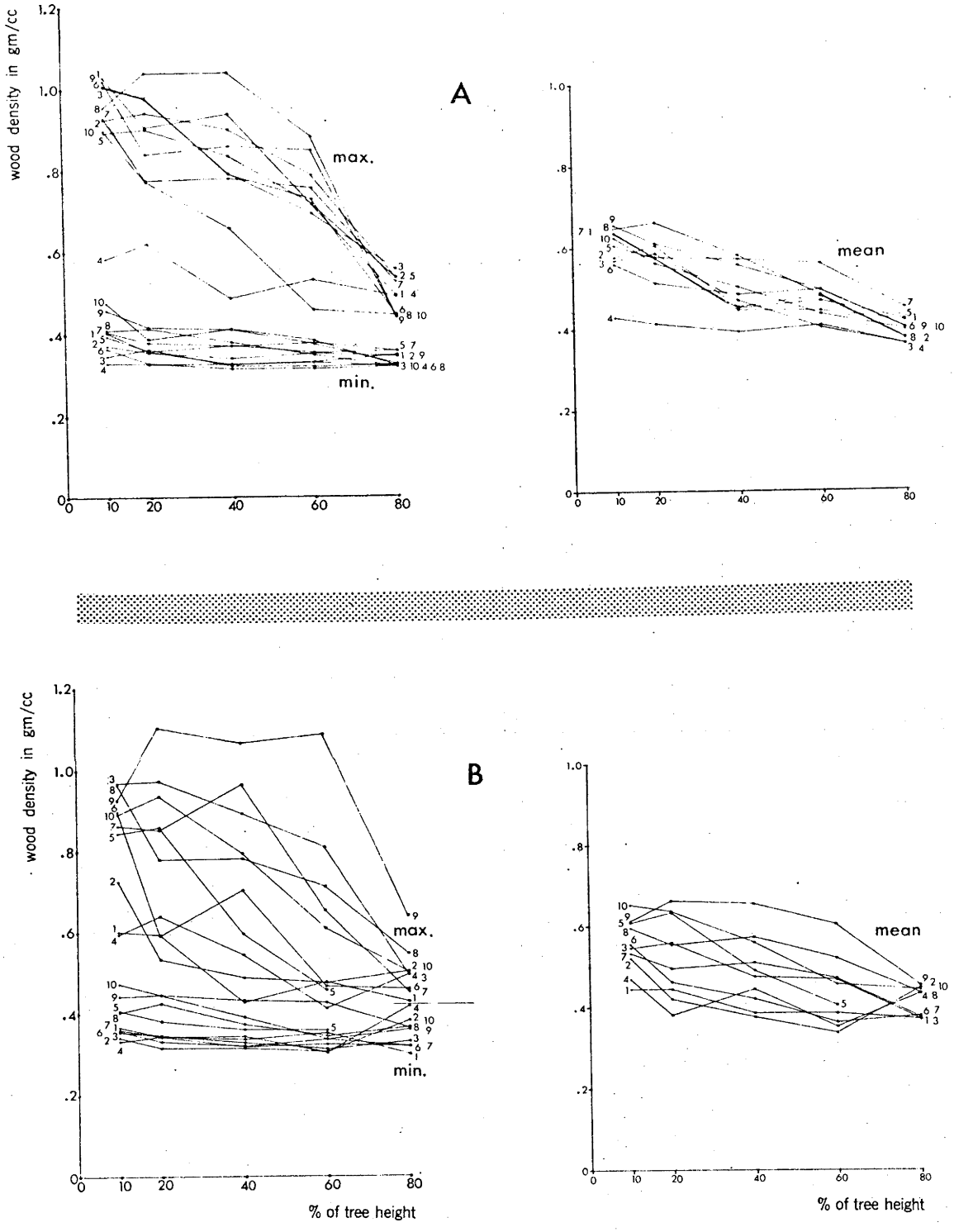


Figure 4.9: Variation with height of maximum, minimum, and mean density of the wood of the third (from bark) annual growth sheath in 10 individual trees from each of sub-plots A and B. Percentile heights are percentages of total tree height at the time of sampling. Individual trees are numbered.

there is an increase in minimum density between 10% and 20% of tree height, whilst in others (A.1, 6, 10; B.5, 6) there is a pronounced decrease. The trends between 60% and 80% of tree height are similarly diverse. No constant systematic trend between trees associated with the absolute value of minimum density is apparent. The pooled estimate for all trees shows a low-order linear decrease of minimum density with height (Table 4.7).

(b). Mean Density

There are large differences between trees in the absolute value of mean density at a given level within the growth sheath. The moderate linear decrease with height of the pooled estimates for all trees (Table 4.7) reflects the general decrease of mean density over the height range in individual trees, but there are pronounced phenotypic differences between trees in the patterns of variation of mean density with height. Within-tree patterns include various degrees of linear decrease with height (e.g., pronounced — A.9, 10; B.10; slight — A.4; B.1), positive (B.9) and negative (B.2) parabolic trends, and less regular trends. There are no consistent systematic trends between trees associated with the absolute value of mean density.

c). Maximum Density

Very large phenotypic differences exist between trees in the absolute value of maximum density at a given level within the growth sheath; the differences being less pronounced at 80% of tree height. For example, the between-tree range of maximum density at 40% of total tree height is 0.43 - 1.07 (0.64) or 83% of the pooled average value (0.77). The very marked contrast in the densitometric characteristics of the trees results in examples where the value of minimum density in one tree (B.9) exceeds maximum density in another (B.4) at a given height (60%) in the corresponding growth sheath. The patterns of variation of maximum density with height are highly variable between trees. With few exceptions (A.4, 10; B.2, 4) there is a marked decrease in maximum density between 60% and 80% of tree height. There are pronounced phenotypic differences between trees in the within-tree range of maximum density. No consistent systematic trend associated with differences in the absolute value of maximum density is apparent. The pooled mean

estimates of maximum density (Table 4.7) show a decreasing linear trend with height to 60% of tree height, and a more pronounced decrease from 60% to 80%.

In many trees (e.g. A.7, 8, 10; B.2, 7, 8, 9, 10) there are similarities in the pattern of variation of maximum and mean density with height, although the variation of mean density is always less pronounced.

At successive levels upwards from the base within an annual growth sheath the wood has been laid down by a cambium of decreasing age. The average age of the cambium (i.e. the average annual ring number from the pith for the 20 trees) at the time of wood formation in growth sheath 3 (from bark) at each height level is indicated in Table 4.7a.

The variation of wood density as a function of age may be examined at a given height in successive annual rings, or, as above, within an annual growth sheath at successive heights. Much of the variation in the latter (oblique) series is associated with radial variation outward from the pith, but possible effects of aging of the apical meristem and variation in the physiological environment associated with height may be superimposed.

Table 4.7a: Mean estimates (20 trees) of ring number (from pith), ring width, and latewood percentage at 6 height levels within the third (from bark) annual growth sheath.

Height in tree	Age from pith (years)	Ring width (mm)		Latewood percentage	
		mean	s.d.	mean	s.d.
Breast height	12	5.42	2.22	55.1	16.9
10%	11.5	5.35	2.13	51.4	23.4
20%	10	5.54	2.18	43.3	19.7
40%	8	6.02	2.35	31.8	18.3
60%	5	8.24	3.14	18.1	14.3
80%	1.5	9.82	2.63	6.81	6.90

An association between crown characteristics and the variation of wood mean density within the oblique series has been demonstrated in Douglas fir (*Pseudotsuga menziesii*) [Harris and Orman, 1958] and radiata pine (*Pinus radiata*) [Richardson, 1961]. Wood density was shown to decrease initially with increasing number of internodes from the stem apex until a minimum value was reached at, or near to, the limit of the live crown, and then to increase progressively. Corroborative evidence for a similar pattern of variation of springwood (earlywood) density in relation to crown features in slash pine (*Pinus elliottii*) is presented by Taras [1965].

The present study is based on a limited percentile height sample rather than a specific pattern of internodal sampling, and thus it is not possible to present an accurate estimate of variation in the upper live crown. But the patterns of variation of wood mean and minimum density with height demonstrated in the third (from bark) annual growth sheath are not related in any consistent way to the measured limits of the live crown. The limit of the live crown (lowest complete green whorl) occurs between 54% and 78% (mean = 68%) of total tree height at the time of sampling. Although there is a general decrease to 60% of total tree height in most trees, the variation of both mean and minimum density between 60% and 80% of tree height is quite variable.

There are formidable difficulties inherent in establishing a measured relationship between crown dimensions (crown size or length) and wood growth that may be interpreted in terms of cause and effect, despite the knowledge that the cambium and the vascular system developing from the cambium exist in an intimate relationship with the foliar organs, both developmentally and functionally. Live branches in the lower crown may be suppressed by shading to an extent where they no longer maintain contact with the main translocation pathways in the tree, and their contribution to stem growth is negligible [see Larson, 1969]. Since neither branch death nor the contribution of different branches to growth is uniform, it is difficult to quantify these relationships.

The variation of wood maximum density within the third growth sheath in the upper stem (in the approximate region of the live crown; i.e., 60% to 80% of tree height at the time of sampling) is more consistent: There is generally a marked depression in the value of maximum density (but cf. trees A.4, 10; B.2, 4, 6). Taras [1965] demonstrated a similar trend with height of summerwood (latewood) density in *P. elliottii*, which was suggestive of crown association.

It is quite possible that the patterns of variation of wood density features with age is, in a large part, a response to physiological changes resulting from the proximity of the site of wood formation to the immediate environment of the live crown. In particular, the proximity to the sites of auxin synthesis in the live crown may affect the development of the wood cells [Larson, 1962]. However, conjectures about the physiological mechanisms underlying the observed patterns of variation of wood features with age remain equivocal. The complex physiology of xylem formation is not well understood, and is known to involve levels of several types of growth promoters, viz., auxin, gibberellins, and cytokinins, operating in the presence of different levels of natural growth inhibitors [see review of Brown, 1970].

The pooled average values of ring width and latewood percentage for the 6 height levels within the third growth sheath are presented in Table 4.7a. In each of these characters there is a pronounced systematic variation with height: As with the densitometric features this is associated with radial variation outward from the pith as a

function of age. The association of mean density with ring width and latewood percentage and their covariation in the complete wood sample was identified and discussed in Section 4.2.

4.3.13. The Variation of the Wood Density of the Annual Growth Increment in Relation to Tree Age

In this sub-section, an attempt is made to define the changes in the density features of the sheath of wood laid down periodically as the tree ages, and to examine the similarities and differences between trees in the trends of change of wood density in successive annual growth increments. Trends of variation of the density features of the annual increment are of practical interest: They provide some indication of the variability and relative magnitude of phenotypic changes and differences that can be attributed to heritable characteristics (e.g., differences between trees in absolute values and patterns of change with tree age), and to environmental influence [e.g., year to year fluctuations). The patterns and the extent of variation have implications for the "plasticity" of response of the wood characteristics of the species to silvicultural manipulation and for selection for breeding response. Elucidation of the relationships between incremental density features and tree growth is important to an understanding of the processes underlying bulk cellulose production. And the data, *per se*, are of interest, particularly in a species which will be used increasingly in tropical areas at crop rotation ages less than the span (18 years) covered in this study.

The computation involved in deriving estimates of the whole-sheath values of the wood characters is heavy: Each of the 20 graphs of Figure 4. 10, for example, is derived from roughly 500 initial measures. But the data, calculations, and plotted output are amenable to real-time processing by electronic digital computer, and programmes were developed to this end.

The weighted values of maximum, minimum, and mean density of each annual growth sheath in each of the 20 trees of sub-plots A and B are shown in Figure 4. 10.

The whole-sheath values were calculated from the ring width and density estimates (average for the 2 sample radii) of the corresponding annual rings (selected from the bark) at individual tree heights corresponding with breast height (1.3 m) and 10%, 20%, 40%, 60% and 80% of total height at the time of sampling.

Stem section volumes were calculated as follows: (i) The stem volume below breast height (1.3 m) was calculated as a right circular cylinder $\left(v = \frac{\pi d^2 h}{4}\right)$; (ii) The volume of each section between the lowest and highest cutting points (discs) was calculated as a right circular cylinder with "end area" of the cylinder equivalent to a simple mean of the two end areas of the stem section; (iii) The volume of the uppermost section of the stem, i.e., from the highest disc (80%) to the stem apex, was calculated as a right circular cone $\left(v = \frac{\pi d^2 h}{12}\right)$. Computations for the basic height-diameter and height-age relationships, from which other tree growth parameters are derived, follow the procedures outlined for stem analysis by Avery [1967].

The procedure for weighting of the density estimates for each annual growth sheath was as follows: The volume of each growth sheath section between discs (v_i) and between the uppermost disc and stem apex, was multiplied by the ring density value of the lower disc (d_i). For the sheath section below breast height the incremental volume was multiplied by the ring density value at breast height. The weighted density estimate (x_{ws}) for each annual growth sheath was derived by dividing the summation of the sheath sectional (volume × density) products by the total sheath volume (v_s). Thus, for each sheath,

$$x_{ws} = \frac{\sum_{i=1}^{6} (v_i . d_i)}{v_s},$$

where,

v_i, d_i are the sheath volume and density values (see text) of the ith stem section,

x_{ws} is the sheath weighted density estimate,

v_s is the total volume of the growth sheath.

The weighted whole-tree estimate of wood mean density was estimated for each successive year of tree growth. The weighted whole-tree estimate (x_{WT}) was calculated as the summation, over sheaths, of the product of the sheath weighted density value and sheath volume, divided by the whole tree volume. Thus,

$$x_{WT} = \frac{\sum_{k=1}^{n} [(x_{ws})_k \cdot (v_s)_k]}{v_T},$$

where,

x_{WT} is the weighted whole-tree estimate of mean density,

$(x_{ws})_k$, and $(v_s)_k$ are the weighted mean density estimate and total volume of the kth annual growth sheath,

v_T is the tree total volume,

n is the number of annual growth sheaths.

Each sheath estimate is thus weighted in relation to the proportion of the whole-tree volume represented by the sheath.

A computer programme, "STANDEN", was developed to facilitate all computations. The computational procedures for the stem-analysis calculations are, in general, similar to those of a stem-analysis programme, "STANAL", developed by D.J. Pluth and D.R. Cameron, University of Alberta [Pluth, Cameron, 1971]. Computer output includes printed output and graphical plots (Figure 4.10). The programme was run on a UNIVAC 1108 computer. Graph plotting was facilitated by storage of digital commands on magnetic tape for operation on a PDP-11 computer with on-line plotting via a CALCOMP 565 graph plotter.

(a). Maximum Density

There are pronounced phenotypic differences between trees in the pattern of variation with age of the weighted whole sheath value of wood maximum density (Figure 4.12). Trends of variation of sheath maximum density with age are highly variable between trees in the young stem (to tree age approximately 8 years). They include: A systematic decrease (trees A.9, 10; B.3, 4, 6); highly variable fluctuations (A.4, 6; B.1, 2, 5, 8); and systematic increase (A.1, 2, 7, 8; B.9, 10).

A.

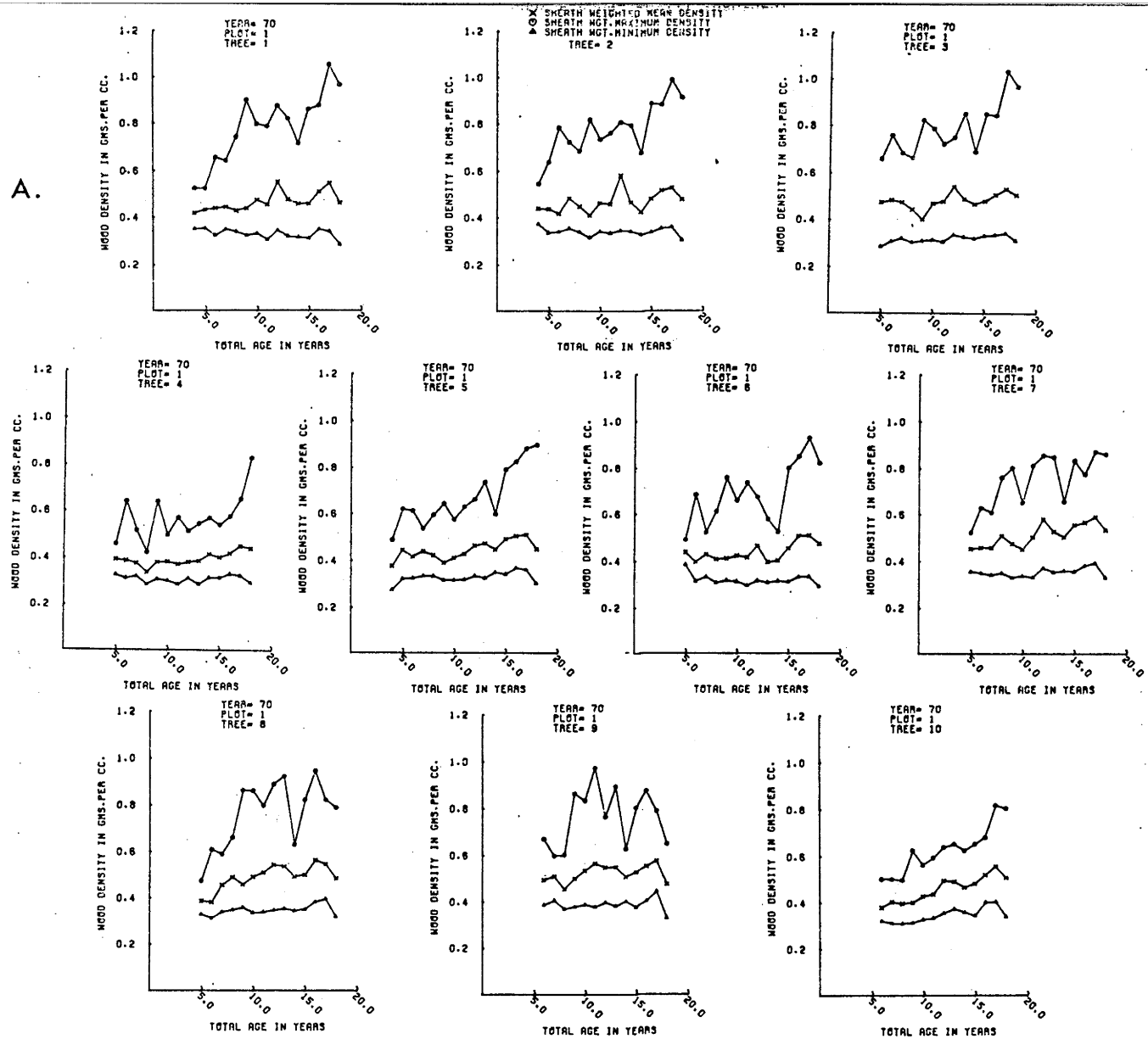
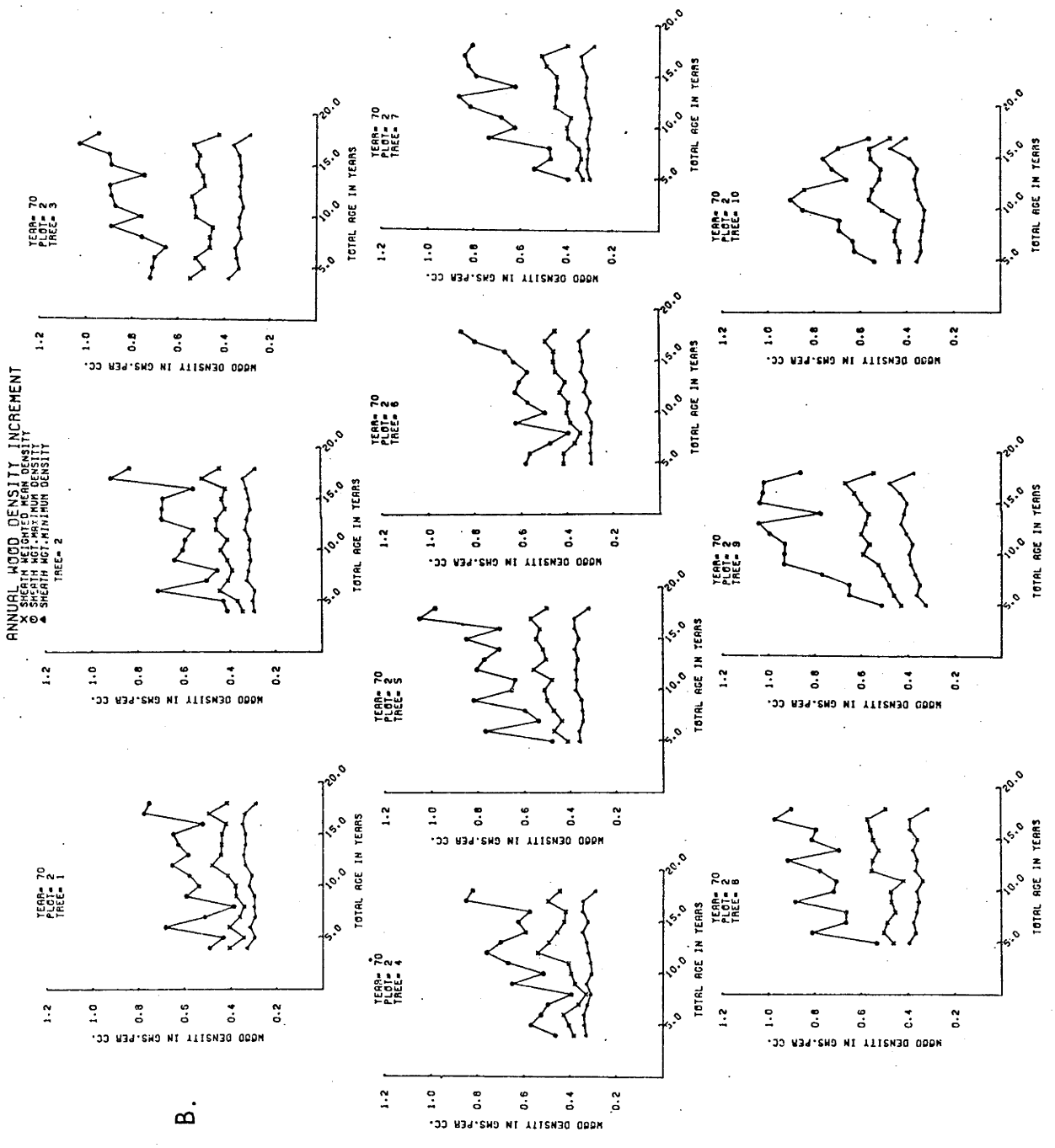

SHEATH WEIGHTED MEAN DENSITY
SHEATH WGT.MAXIMUM DENSITY
SHEATH WGT.MINIMUM DENSITY
YEAR= 70
PLOT= 1
TREE= 1
TREE= 2
TREE= 3
TREE= 4
TREE= 5
TREE= 6
TREE= 7
TREE= 8
TREE= 9
TREE= 10
WOOD DENSITY IN GMS.PER CC.
TOTAL AGE IN YEARS
1.2
1.0
0.8
0.6
0.4
0.2
5.0
10.0
15.0
20.0

Figure 4.10: Variation with age of the weighted estimates of maximum, minimum, and mean density of the wood of each annual growth sheath in each of the 20 trees of sub-plots A (plot 1) and B (plot 2). Total age refers to the number of years since seedling transplant (1952). The outermost growth sheath corresponds with tree age 18 years. Individual trees are numbered.



Thereafter there is a general systematic increase in sheath maximum density with age in most trees. In some trees (A.8, 9; B.7, 9, 10) the overall trend is quadratic, i.e., the sheath weighted value of maximum density increases with age to a maximum, and then decreases. This quadratic trend is more pronounced, and the maximum value is reached at an earlier age (11 years; cf., 13 years in B.7, 9, and 16 years in A.8), in the more highly suppressed trees, viz., A.9 and B.10 (see growth data of sub-section 4.6). The trend of increase of sheath maximum density with age is essentially linear, though highly irregular, in all the more vigorous trees. Pronounced phenotypic differences between trees in the rate of increase of sheath maximum density with age appear to bear little relation to tree vigour (cf. volume increments — Figure 4.16).

The systematic trends of variation of sheath maximum density with sheath age reflect the increase in maximum density of wood laid down by a cambium of increasing age (N.B., within the annual growth sheath the age of the cambium increases basipetally with each successive annual height increment). Genotypic differences between trees with comparably vigorous growth presumably underly the differences in response of maximum density to the physiological changes associated with age ("age" being a function of position effects related to the proximity of the site of wood formation to the active regions of the living crown).

The marked irregularities in the curves, which represent radical changes in the sheath weighted maximum density from year to year, presumably reflect response to environmental influences. There is an element of similarity of response of the trees in certain years: Thus, for example, maximum density is high in sheath 2 (from bark) and always depressed in sheath 5. But the response is highly variable between trees in many of the annual growth sheaths, particularly the inner sheaths. To the extent that these responses are heritable, they reflect considerable genotypic differences between trees in the response to particular environmental influences.

There are very considerable differences between trees in the absolute value of the maximum density within corresponding growth sheaths.

The systematic increase in the pooled average estimate of sheath weighted maximum density with age follows an essentially linear trend (Figure 4.11). The curve is highly irregular.

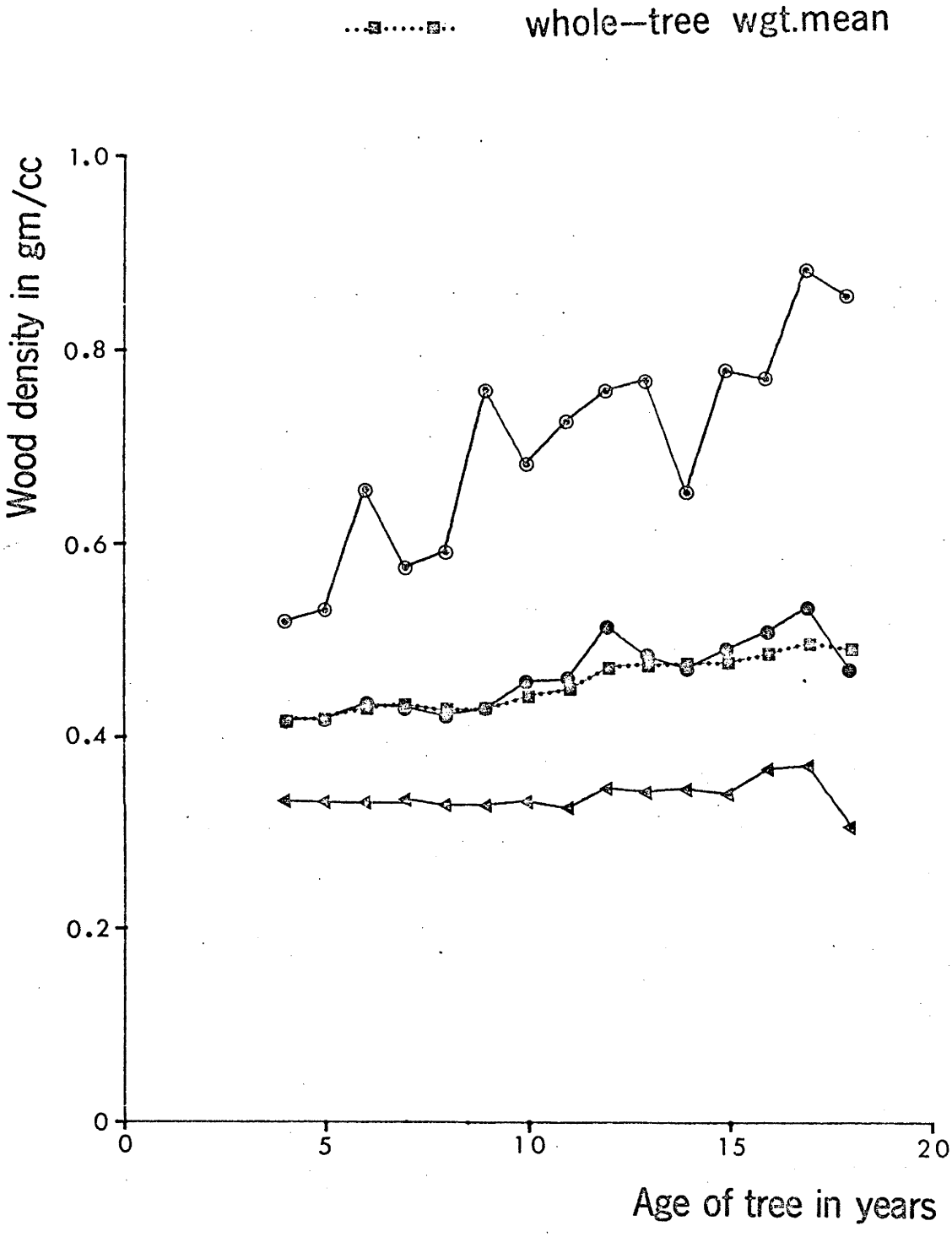


Figure 4.11: The variation of the pooled estimates of the weighted values of maximum, mean, and minimum density of the wood of successive annual growth sheaths, and of the weighted whole-tree value of wood mean density, in relation to tree age. Each point on the curves represents the simple arithmetic mean of the value at corresponding ages in 20 trees. Total age refers to the number of years since seedling transplant (1952).

b). Minimum Density

The variation with age of the weighted whole sheath value of minimum density is very much less pronounced than the corresponding variation of maximum density (Figure 4. 10). Minimum density remains almost constant with age in most trees. In some trees there is a systematic increase in sheath minimum density with age; this trend is most pronounced in the outer sheaths of trees of low vigour (e.g. A.10; B.9, 10). There is no consistent trend of variation of minimum density in the inner sheaths. Fluctuations in the value of sheath minimum density from year to year are relatively minor.

The range of difference between trees in the weighted whole sheath value of minimum density at a given age is a considerable proportion of the mean value.

The pooled average estimate of sheath weighted minimum density (Figure 4.11) remains constant (approximately 0.33) to age 11 years (sheath 8 – from bark), then increases to a maximum (0.37) at 17 years (sheath 2). There is an abrupt depression of sheath minimum density (0.31) in the outermost growth sheath. The depression of minimum density in the sheath next to the bark is a consistent feature (Figure 4. 10), but is most abrupt in trees of low vigour (A.8, 9, 10; B.8, 9, 10 – cf. volume increments in sub-section 4.6; Figure 4.16). The effect is exaggerated in the pooled estimate, since the estimate is a simple arithmetic mean of the sheath values of all trees, i.e., the relative amount of wood corresponding to each tree value is not taken into account in the calculation of the pooled estimate. The increase in the pooled estimate from age 12 years will be similarly exaggerated.

(c). Mean Density

There are considerable differences between trees in the pattern of variation with age of whole-sheath weighted mean density, and in the mean density of corresponding growth sheaths (Figure 4.10). Trends of variation in the inner sheaths, to age approximately 8 years, are highly variable. Thereafter there is a general linear increase in mean density with sheath age; the rate of increase being highly variable between trees.

Fluctuations in the value of sheath mean density from year to year are considerable. Some of the annual fluctuations are consistent between trees (e.g., mean density of sheath 7 (from bark) is consistently high; sheath 5 generally low), reflecting an element of consistency of response of trees to environmental change.

The variation with age of whole-tree mean density (Figure 4.12) is highly variable between trees in the young stem. From an age of approximately 8 years there is a general linear increase with tree age.

The pooled average estimate of weighted mean sheath density (Figure 4.11) remains relatively constant (0.42) with age to 9 years (sheath 10 from bark); thereafter there is a general linear trend of increase with age (maximum value 0.53 — sheath 2). The pooled estimate of weighted whole-tree mean density shows a similar trend (Figure 4.11) from 0.42 (age 4) to 0.49 (age 18).

A.

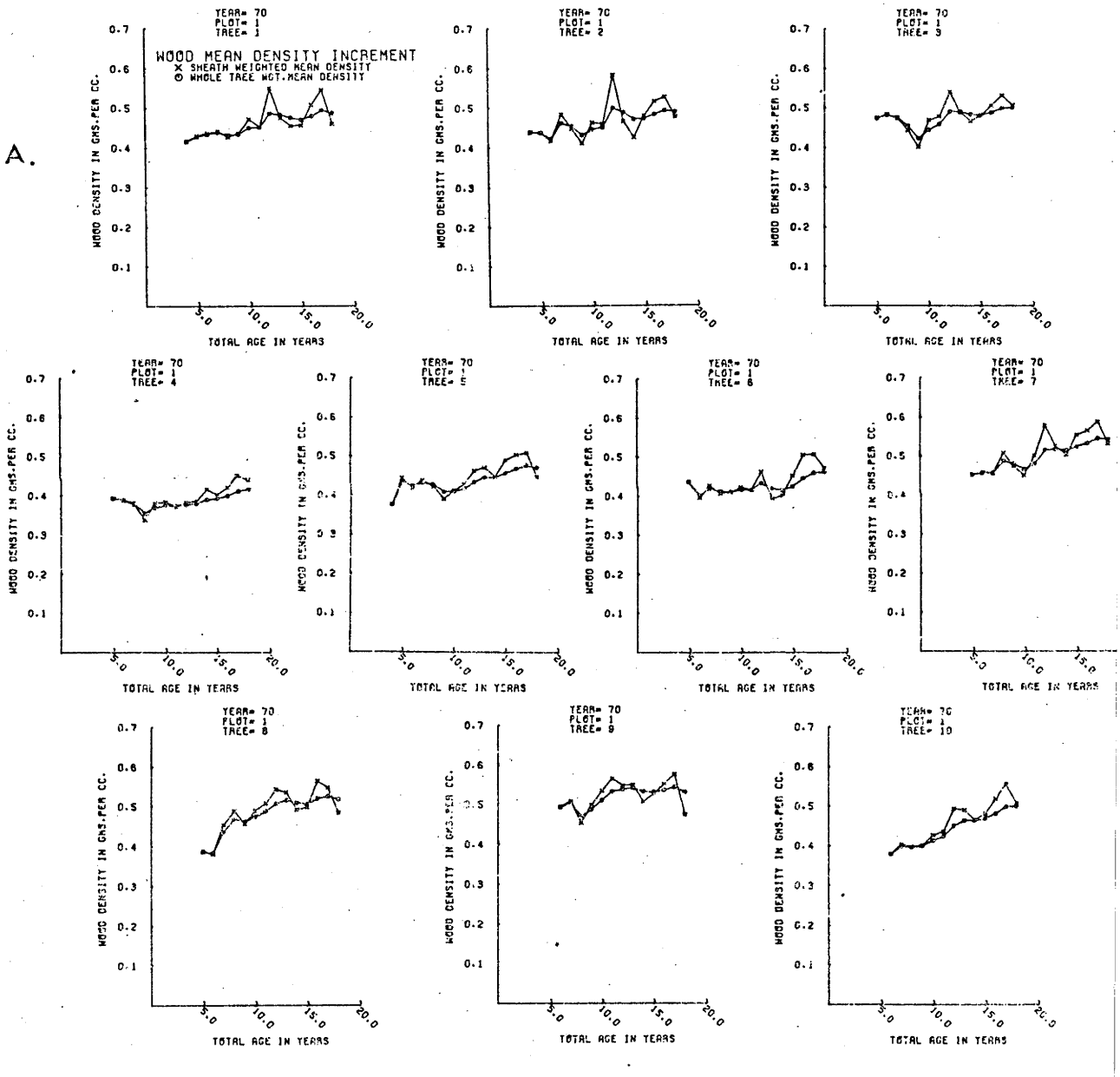
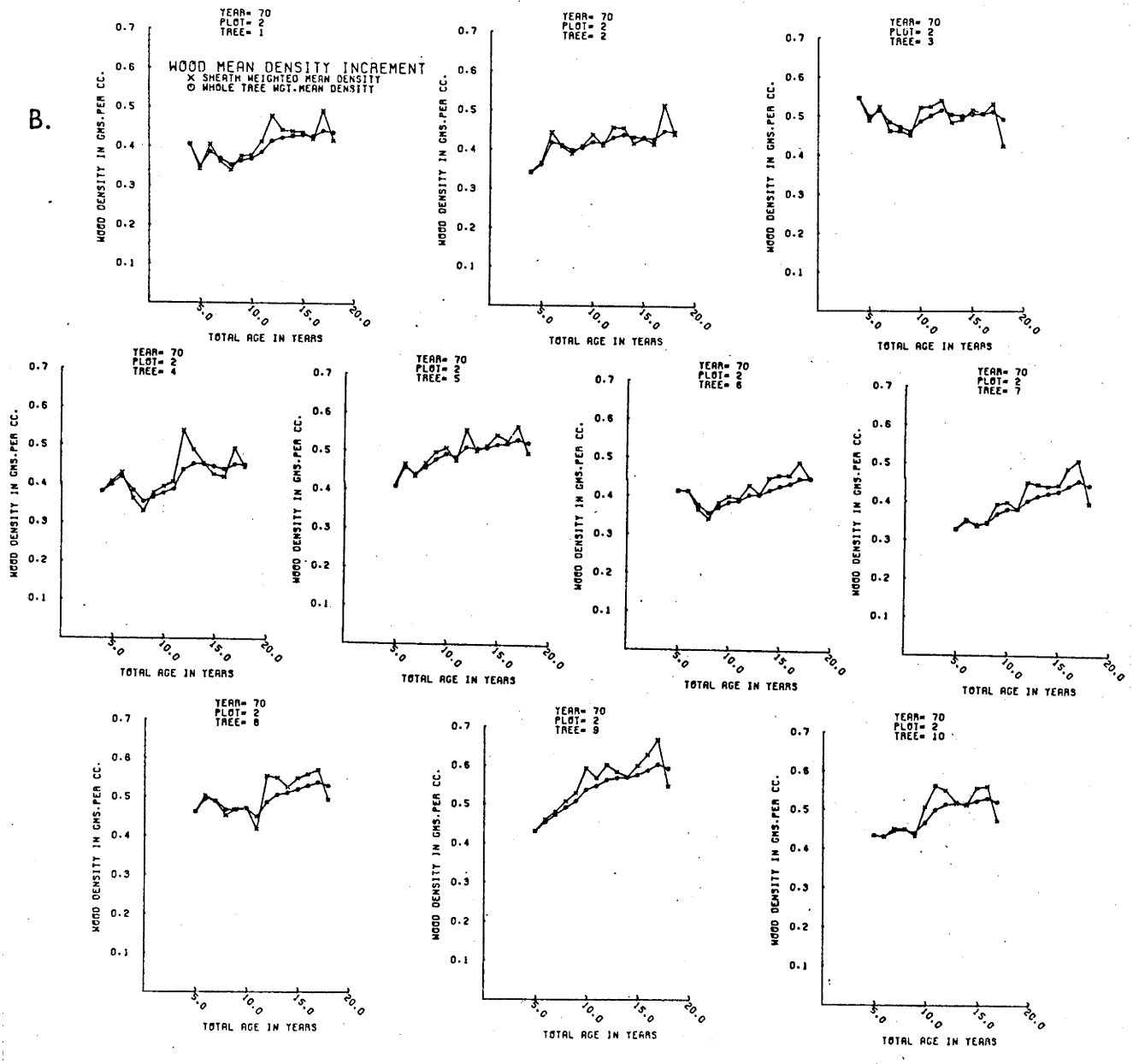

YEAR= 70
PLOT= 1
TREE= 1
WOOD MEAN DENSITY INCREMENT
X SHEATH WEIGHTED MEAN DENSITY
⊙ WHOLE TREE WGT.MEAN DENSITY
WOOD DENSITY IN GMS.PER CC.
TOTAL AGE IN YEARS
YEAR= 70
PLOT= 1
TREE= 2
YEAR= 70
PLOT= 1
TREE= 3
YEAR= 70
PLOT= 1
TREE= 4
YEAR= 70
PLOT= 1
TREE= 5
YEAR= 70
PLOT= 1
TREE= 6
YEAR= 70
PLOT= 1
TREE= 7
YEAR= 70
PLOT= 1
TREE= 8
YEAR= 70
PLOT= 1
TREE= 9
YEAR= 70
PLOT= 1
TREE= 10

Figure 4.12: Variation with age of the weighted estimates of the mean density of each complete annual growth sheath and the whole-tree in each of the 20 trees of sub-plots A (plot 1) and B (plot 2). Total age refers to the number of years since seedling transplant (1952). The outermost growth sheath corresponds with tree age 18 years. Individual trees are numbered.

B.



4.3.2. THE SYSTEMATIC VARIATION OF TRACHEID CROSS-SECTIONAL DIMENSIONS WITHIN THE STEM

A Review of the Literature

The study of variation in the cross-sectional dimensions of wood cells is an area of wood science that has received relatively scant attention when compared with the extent of research effort and the voluminous literature devoted to the study of wood density and tracheid length. The neglect of research effort in this area is generally attributed to the tedious and time-consuming nature of the measurements involved and the lack, until recently, of standard techniques to yield sufficiently precise estimates of the wall and lumen dimensions of tracheids for effective comparative study [see, e.g., Taras, 1965]. Recent technological advances in measurement technique [see Smith, 1965] have largely overcome the latter problem and alleviated the former to some considerable extent.

A knowledge of the variation in tracheid cross-sectional dimensions in conifers is fundamental to an understanding of the mechanisms underlying the variation of other wood characteristics. Such characters, and in particular wood density, are used extensively as indices of wood quality, i.e., of the suitability of the wood for a wide range of uses (see Chapter 3).

There is an urgent need for more information on the variation and pattern of inheritance of the anatomical components of basic density [see Zobel, 1961]. This requirement is of acute significance to tree improvement programmes involving breeding for wood density features *per se*, because the anatomical components of basic density (viz., tracheid wall thickness and lumen width) are under independent physiological control [Larson, 1960; Richardson, Dinwoodie, 1960; Wodzicki, 1964; Balatinecz, Kennedy, 1968]. Maximum efficiency in breeding cannot be achieved until the anatomical variation and the processes controlling it are better understood [see Richardson, 1960; Zobel, 1961; Waering, 1964].

In the technology of pulp and papermaking there is increasing evidence that tracheid cross-sectional dimensions influence paper properties to a greater extent than tracheid length [Dinwoodie, 1965; van Buijtenen, 1969; Panshin, de Zeeuw, 1970], and these anatomical traits are known to affect a range of properties important to wood utilisation such as strength, shrinkage and swelling, permeability, gluing and pulping and machining characteristics [Goggans, 1965; Orman, Harris, 1965; van Buijtenen, 1969]. As a consequence, the urgent need for an increased general understanding of the variation of tracheid cross-sectional dimensions in coniferous wood has been expressed with specific regard to technological application, e.g., in pulp and paper research [see, e.g., Tappi, 1960; Schultz-Dewitz, 1965].

Studies of within-tree variation of tracheid C.S. dimensions are very limited, and a comparative evaluation of results is complicated by the wide variety of methods of measurement used [see review of Taras, 1965, pp.18-20]. Reports are largely confined to estimates of variation of tracheid C.S. dimensions in the horizontal plane. Many reports have involved the study of variation in one or a very few trees, and generally at one level in the lower stem (near breast height). An exception is the study of variation of tracheid dimensions at four height levels (10% to 60% of tree height) in ten trees of *Pinus caribaea* from a natural stand at Mt. Pine Ridge, British Honduras [Lantican, 1972]. The results of this study are of especial relevance to those of the present investigation: They provide valuable comparative and supplementary information about the variation of these wood characteristics in the species.

Cross-Sectional Dimensions of Earlywood Tracheids

Earlywood Tracheid Wall Thickness

Radial wall thickness has been shown to increase outwards from the pith in a range of coniferous species, e.g., *Larix decidua*, *Pinus sylvestris*, *P. mugo* [see Goggans, 1965], *P. resinosa* [Larson, 1966], *P. echinata* [Panshin, de Zeeuw, 1970], and *P. caribaea* var. *hondurensis* [Lantican, 1972]. An increase in wall thickness (the sample not differentiating early- and latewood cells) radially was reported in

12-year old *P. caribaea* var. *caribaea* from Cuba [Burley, Hughes, Lamb, 1972]. Wall thickness of earlywood tracheids was reported to be unaffected by age from pith in *Pinus elliottii* [Taras, 1965], *Picea excelsa*, and *Pseudotsuga menziesii* [see Schultz-Dewitz, 1965], and *Pinus taeda* [McMillin, 1968].

Very few studies have been made of the variation of wall thickness in the axial plane. Larson [1966] reported little difference in wall thickness between the 6 foot- and 18 foot-level in a single tree of *Pinus resinosa*. Burley *et al.* [1972] reported no practically significant differences between trees or height levels (5% and 65% of tree height) in the mean values of tracheid wall thickness (early- and latewood not distinguished) for the inner six rings in two trees of *P. caribaea* var. *caribaea* from Cuba. Radial and tangential double-wall thickness were shown to remain more or less constant with height (10% to 60%) in *P. caribaea* var. *hondurensis* [Lantican, 1972]: The average value was slightly greater for radial than tangential double-wall thickness at any height level.

Earlywood Tracheid Lumen Width and Cell Diameter

In breast-height samples from 3 trees of *Pinus elliottii*, Taras [1965] demonstrated an increase in both lumen width and cell diameter of earlywood tracheids outward from the pith; rapidly from pith to age about 12 years, then more slowly to age approximately 20 years after which the dimensions remained constant with age. Radial lumen and cell widths have been reported to increase with age from the pith in *Pinus sylvestris*, *P. mugo*, *Larix decidua* [see Goggans, 1965], *Pseudotsuga menziesii* [Schultz-Dewitz, 1965], and in *Pinus taeda* [McMillin, 1968]. Burley *et al.* [1972] report that lumen diameter (early- and latewood not distinguished) remained effectively constant up to 12 rings from the pith at 5% of tree height in 2 trees of *Pinus caribaea* var. *caribaea*. Earlywood lumen width and cell diameter increased outward from the pith, but at a decreasing rate in *P. caribaea* var. *hondurensis* [Lantican, 1972]: Radial lumen width was greater than tangential lumen width regardless of ring number. Relatively slight changes in these characters occurred in the axial direction: Lumen width increased by approximately 7% from 10% to 20% of tree height, then remained more or less constant to 60% of tree height.

Significant between-tree variation in the cross-sectional dimensions of earlywood tracheids have been reported in *Pinus elliottii* and *P. taeda* from Queensland [see Smith, 1967], and in young (5 to 6-year old) *P. taeda* from Louisiana [Goggans, 1962].

Cross-Sectional Dimensions of Latewood Tracheids

Latewood Tracheid Wall Thickness

A general quadratic pattern of increase of radial double-wall thickness with age from the pith has been demonstrated in a number of coniferous species. In breast-height samples from 3 trees of *Pinus elliottii* latewood wall thickness was shown to increase fairly rapidly for the first 10 years, the rate of increase then decreasing before levelling off at about age 22 years [Taras, 1965]. A quadratic trend of increase of wall thickness with age was noted in *Pinus resinosa* [Larson, 1966], *P. taeda* [McMillin, 1968], and in *P. echinata* [see Panshin, de Zeeuw, 1970]. In *P. caribaea* var. *hondurensis* wall thickness of the latewood tracheids increased rapidly from ring 2 to 14; subsequent variation outward from the pith was relatively slight, with a peak value attained at rings 17 - 20 [Lantican, 1972].

Little is known of the general trends of variation of latewood tracheid wall thickness in the axial direction in conifers. Larson [1966] reported very little variation in radial wall thickness between the 6-foot and 18-foot level in a single tree of *P. resinosa*. A linear decrease in the radial wall thickness of latewood tracheids with height was demonstrated in *P. elliottii* and *P. taeda* [Hiller, 1964]. In *P. caribaea* var. *hondurensis* radial wall thickness decreased linearly with height, but tangential wall thickness showed no significant change in the axial direction [Lantican, 1972]: Radial dimensions were, in general, smaller than their tangential counterparts.

Latewood Tracheid Lumen Width

Little is known of patterns of variation of the lumen width of latewood tracheids within the stems of conifers. McMillin [1968], in a study of 50 trees of *Pinus taeda*, found no significant change in this

character with age from pith. The tangential diameter of latewood tracheids showed a decreasing trend to about age 10 years and then a definite but slight increase with age in 3 trees of *P. elliottii* at breast height [Taras, 1965]. Lantican [1972] demonstrated a quadratic trend of decrease in latewood lumen width with age from the pith: The decrease was fairly rapid from rings 2 to 14 but became smaller with increasing age, reaching a minimum value at rings 17 - 20. There was a quadratic trend of decrease in radial lumen diameter with height (10% to 60%), but tangential lumen diameter remained constant with height.

Latewood Tracheid Width

The tangential diameter of latewood tracheids at breast height in 3 trees of *Pinus elliottii* was shown to increase outward from the pith at a uniform rate to ring 26 - 28, and thereafter to remain constant [Taras, 1965]. A low-order increase in radial cell width with age from the pith has been reported in *P. taeda* [Wheeler, Zobel, Weeks, 1966; McMillin, 1968]. Schultz-Dewitz [1958; see Goggans, 1965] found latewood tracheid diameter highly variable, with a tendency to fluctuate from pith to bark in two *Pinus* species (*P. sylvestris*, *P. mugo*) and in *Larix decidua*. In *Pinus caribaea* var. *hondurensis*, Lantican [1972] found the radial width of latewood tracheids to be unaffected by age from the pith at each of 4 height levels (10% - 60%). In contrast, tangential cell width increased outward from the pith; the rate of increase with age was relatively rapid to ring 14, but steadily diminished with increasing age. The radial width of latewood tracheids decreased quadratically with increasing height, but there was no significant change in tangential cell width in the axial direction.

Considerable differences between trees in radial and tangential cell widths have been reported in *Pinus taeda* [Goggans, 1962; Posey, 1964]. Smith [1967] reported a high degree of between-tree variation of radial cell width in *P. elliottii* and *P. taeda* grown in Queensland.

Differences in the relative values of the radial and tangential cross-sectional dimensions of the tracheids in the earlywood and latewood were demonstrated in 30-year old trees of *Pinus caribaea* from British Honduras [Lantican, 1972]. In the earlywood, the radial dimensions of the tracheids generally exceeded their tangential counterparts, whilst

the converse applied in the latewood cells. Dissimilar patterns of radial and tangential cell widths were demonstrated in both the axial and radial planes, indicating that tracheid C.S. shape varies with height and age from the pith.

Results and Discussion

4.3.21. The Variation of Tracheid Cross-Sectional Dimensions with Height in the Tree

21.1. The Variation of the Average Tracheid Dimensions of the Stem Cross-Section with Height

The arithmetic average disc values of double-wall thickness and lumen diameter of earlywood and latewood tracheids for the five percentile levels from breast height to 60% of total tree height are presented in Figure 4.13. The values were calculated from a sample comprising measures of rings 3, 7, and 11 (from bark) at each level where these rings were visually distinguished (see Section 4.2 for a description of the sample). The system of arithmetic averaging is described in Section 4.4.

The average pooled estimates for all trees are shown in Figure 4.13. Errors associated with these estimates are presented in Tables 4.13 a - f.

(a). Latewood Tracheid Wall Thickness and Lumen Diameter

There is a low-order systematic decrease in the pooled average estimate of tracheid double-wall thickness with percentage of tree height, the decrease being greatest between 10% and 20%.

There are pronounced phenotypic differences between trees in the absolute value of this character at a given height, and in the pattern of variation with height (see Figure 4.13). Major irregularities in the curves could result from the effect of variation between radii of each disc and/or from measurement error, since the sample comprises a

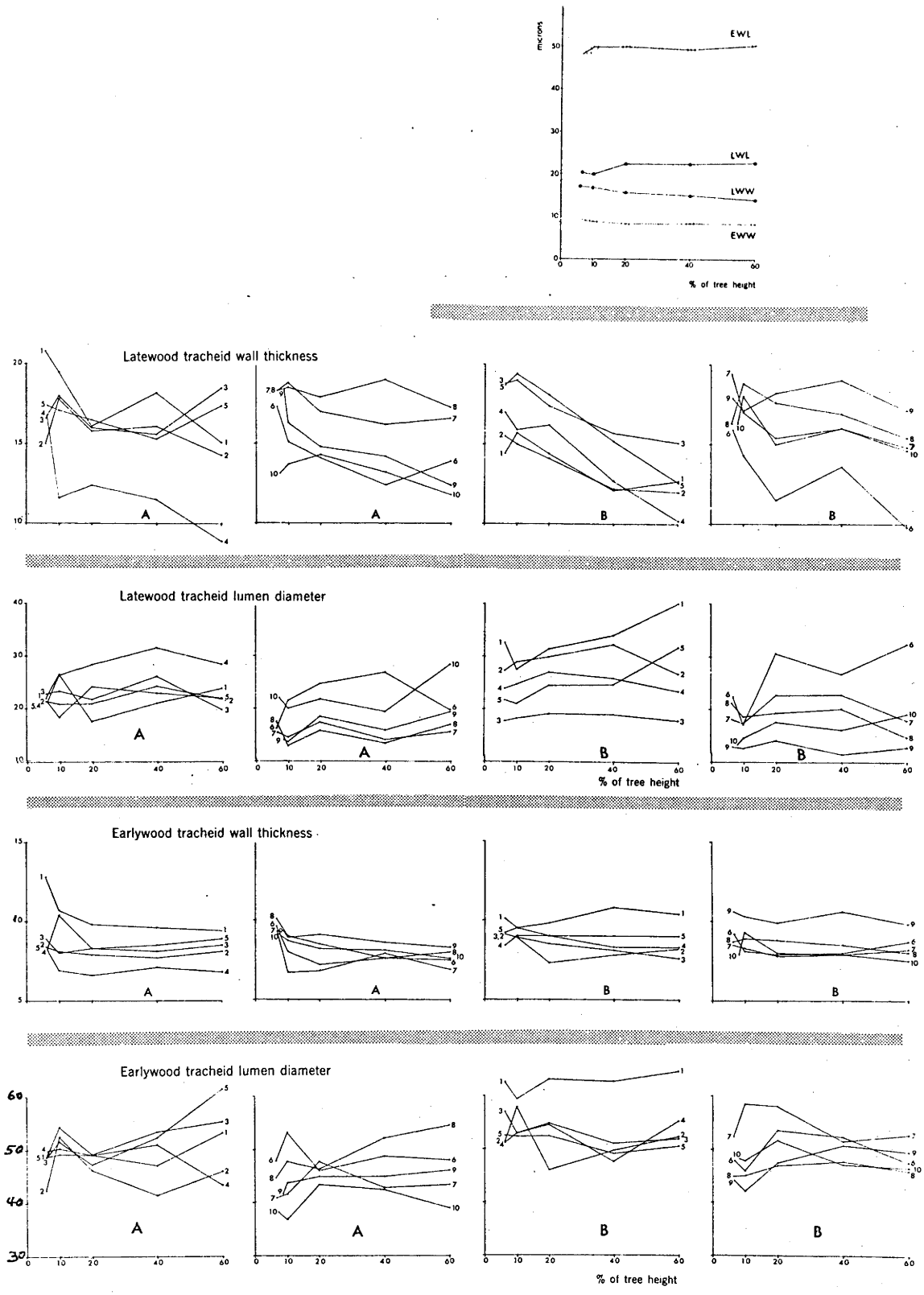


Figure 4.13: The variation with height of the arithmetic average disc values of double-wall thickness and lumen diameter of earlywood and latewood tracheids in each of the 20 trees (A.1 - 10; B.1 - 10).

The average estimates from the pooled data of the 20 trees are shown in the uppermost figure.

limited number of rings from one radius per disc (Section 4.2).

The pooled average estimate of latewood tracheid lumen diameter increases from 10% to 20% of tree height, then remains constant to 60% of tree height.

There are considerable differences between trees in the value of this character. In general, there is a complementary relationship between trees in the relative value of wall thickness and lumen diameter; i.e., trees with thick cell walls tend to have narrow cell lumens, and this relationship holds at all heights. This indicates a large between-tree component in the variation of the contrast between wall thickness and lumen diameter.

The variation of lumen diameter with height within individual trees is, in general, less pronounced than the corresponding variation of wall thickness. The trends of variation of these two characters with height may complement one another; e.g., trends for wall thickness and lumen diameter, respectively, are: Negative and positive quadratic (tree A.6), positive and negative quadratic (A.10).

(b). Earlywood Tracheid Wall Thickness and Lumen Diameter

The pooled average estimate of earlywood tracheid wall thickness decreases slightly to 20% of tree height and then remains constant to 60% of tree height.

In most trees the wall thickness remains relatively constant with height; the main differences between trees in the trend occurring in the lower stem. The major part of the variation between trees is in the absolute value of this character at a given height.

The pooled average estimate of earlywood tracheid lumen width remains almost constant with height; the variation being a negligible portion of the mean of approximately 50 microns, or over 5X the pooled estimate of double-wall thickness.

Within individual trees the lumen diameter tends to remain relatively constant with height, but there are irregularities which may reflect measurement or sample errors (see discussion of latewood cells). A large component of the variation is associated with differences in the absolute value of lumen diameter between trees. There is no consistent relationship between trees in the relative value of wall thickness and lumen diameter; e.g., thick-walled tracheids may be associated with wide lumens (in tree B.1) or narrow lumens (in tree B.9).

The slight to negligible change in the average values of wall thickness and lumen width of the earlywood tracheids in the axial direction accord with the findings of Lantican (1972), who demonstrated an effectively similar pattern of axial variation in these parameters in a sample of 10 trees of *P. caribaea* var. *hondurensis* from a natural stand at Mt. Pine Ridge, British Honduras.

The essentially linear decrease in the radial wall thickness of the latewood tracheids with height is in agreement with the findings of Lantican [1972], but differing patterns of variation of the radial lumen width of latewood tracheids in the axial plane were found in the two studies. In this study lumen width was shown to increase in the lower stem to 20% of tree height then remain constant to 60% of tree height, whereas in the material from Mt. Pine Ridge [Lantican, 1972] there was a quadratic trend of decrease in radial lumen diameter with height (10% - 60%).

It is evident from a comparison of the ranking of the trees on the scales of lumen diameter in Figure 4.13 with the growth data for the individual trees presented in sub-section 4.6 (Figures 4.16 and 4.17) that the latewood tracheids of the more vigorous trees tend to have wider lumens. There is a similar, though weaker, relationship of tree vigour with earlywood tracheid lumen width. No such relationship between overall tree vigour and wall thickness of either the latewood or earlywood tracheids is evident (see Figure 4.11, also).

2. The Variation of Tracheid Cross-Sectional Dimensions with Height Within An Annual Growth Sheath

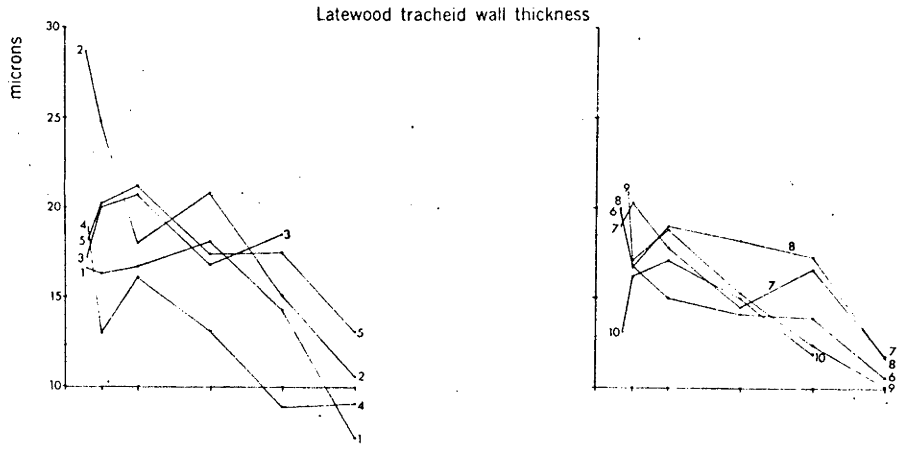
The variation, in relation to percentage of total tree height, of the radial double-wall thickness and lumen width of latewood and earlywood tracheids within the third growth sheath from the bark, in the 10 trees of sub-plot A, is shown in Figure 4.14. The pooled average estimates (10 trees) are presented in Table 4.8.

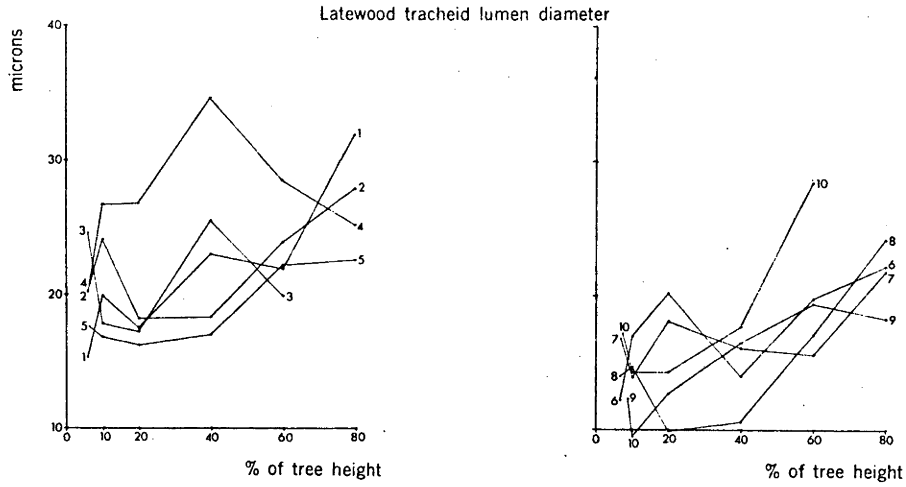
. Latewood Tracheid Wall Thickness and Lumen Width

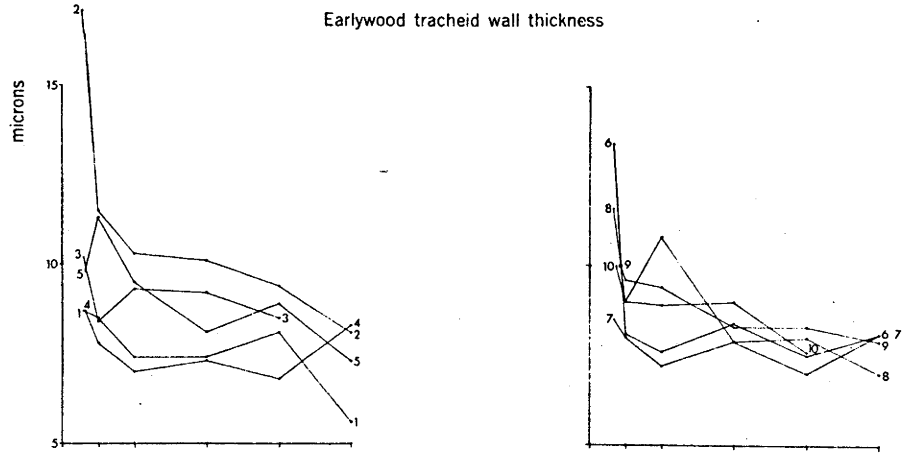
There is a marked systematic decrease with height of the pooled estimate of latewood tracheid wall thickness (Table 4.8).

Within individual trees there is a general decrease in wall thickness over the height range, but there are considerable phenotypic differences between trees in the patterns of variation of this character

Figure 4.14: Variation with height of tracheid double-wall thickness and lumen diameter within the earlywood and latewood regions of the wood of the third (from bark) annual growth sheath in the 10 trees of sub-plot A. Percentile heights are percentages of total tree height at the time of sampling. Individual trees are numbered.


Latewood tracheid wall thickness
microns
30
25
20
15
10


Latewood tracheid lumen diameter
microns
40
30
20
10
0
10
20
40
60
80
% of tree height
% of tree height


Earlywood tracheid wall thickness
microns
15
10
5

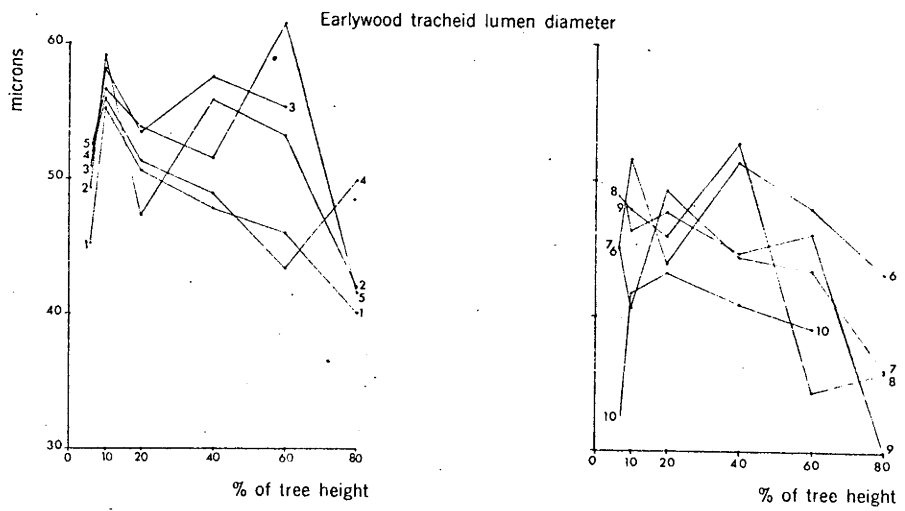

Earlywood tracheid lumen diameter
microns
60
50
40
30
0
10
20
40
60
80
% of tree height
% of tree height

Table 4.8: Mean values (10 trees of sub-plot A) and standard deviations of double-wall thickness and lumen diameter (microns) in the latewood and earlywood regions of the wood at six height levels within growth sheath 3 (from bark). Percentile heights refer to percentage of total tree height at the time of sampling.

Height in tree	LATEWOOD				EARLYWOOD			
	Double-wall thickness		Lumen diameter		Double-wall thickness		Lumen diameter	
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Breast height	19.25	3.99	17.10	3.94	10.80	2.66	46.96	5.76
10%	18.14	3.25	17.47	5.05	9.12	1.32	51.30	6.79
20%	18.04	1.95	17.11	4.55	8.74	1.36	48.64	3.70
40%	16.33	2.35	19.33	6.81	8.36	.86	49.57	5.25
60%	14.64	2.99	21.67	4.30	8.01	.81	47.04	7.94
80%	10.53	1.81	24.26	4.16	7.55	.91	39.85	5.94

with height (Figure 4.11). There is a consistent decrease in wall thickness only between 60% and 80% of tree height. Between breast height and 20% of tree height the change in wall thickness is highly variable between trees; some trees exhibiting a pronounced decrease (A.2, 6), others an increase (A.3, 5, 10).

Some irregularities in the curves (Figure 4.11) could result from the effect of variation between radii of each disc and/or from measurement error, since one radius was sampled at each level.

Considerable between-tree differences in wall thickness at a given height are evident.

The pooled average estimate of latewood tracheid lumen diameter remains constant to 20% of tree height then increases systematically with height between 20% and 80% of tree height.

With the exception of tree A.4, the variation of lumen diameter with height within the growth sheath shows considerable diversity between trees in the lower bole but a more or less regular increase from 20% to 80% of tree height. There is a pronounced quadratic trend of variation

of lumen diameter with height in tree A.4; i.e., the value increases to a maximum at 40% of tree height and then decreases.

There are considerable differences between trees in the lumen diameter at a given level.

In general, there is a complementary relationship between trees in the relative value of latewood wall thickness and lumen diameter; i.e., trees with thick-walled cells tend to have narrow cell lumens, and this relationship holds over the height range. This indicates a considerable between-tree component in the variation of the contrast between wall thickness and lumen diameter of the latewood cells.

Earlywood Tracheid Wall Thickness and Lumen Width

There is a systematic decrease in the pooled average estimate of earlywood tracheid double-wall thickness with height (Table 4.8).

There is considerable variation between trees in the pattern of variation of wall thickness; the differences being most pronounced in the lower stem from breast height to 20% of tree height. In most trees there is a more or less regular gradual decrease from 20% to 80% of tree height (Figure 4.14).

Some similarities in the patterns of variation with height of wall thickness of the earlywood and latewood cells of corresponding trees are apparent (see in particular trees A.2, 4, 6), but the variation with height, particularly in the upper stem, is always much more pronounced in the latewood cells (note the differences of scale in Figure 4.14).

The between-tree range of double-wall thickness at a given level is a considerable portion of the mean tree value. There is a general similarity in the relative values of the latewood and the earlywood measures between corresponding trees.

Considerable phenotypic differences between trees in the pattern of variation of earlywood tracheid lumen width with height are evident (Figure 4.14). The curves are markedly irregular: This may, to some extent, reflect radial variability at a given level, since only one radius per level was sampled. Within many trees (e.g. A.2, 3, 5, 6, 7, 9) the lumen diameter remains relatively constant to 60% of tree height, and decreases sharply between 60% and 80% of tree height.

There are considerable between-tree differences in lumen diameter at a given height.

The pooled average estimate of earlywood tracheid lumen diameter increases from breast height to a maximum at 10% of tree height, then decreases with height, gradually to 60% of tree height, and abruptly from 60% to 80% of tree height (Table 4.8).

4.3.22. The Variation of Tracheid Cross-Sectional Dimensions Outward from the Pith

Parametric estimates of the cross-sectional dimensions of the latewood and earlywood tracheids in the third, seventh, and eleventh annual growth rings from the bark* at six height levels are presented in Tables 4.9 and 4.10 respectively. The estimates were derived from the pooled data of 20 trees.

The variation of the average values of each of the anatomical characteristics within both the horizontal and the oblique series is presented in these tables. The variability between trees in the patterns of variation of each of these characters within the oblique series was discussed in sub-section 4.3.21.2.

2.1. Radial Cross-sectional Dimensions of the Latewood Tracheids

a). Latewood Tracheid Double-Wall Thickness

There is a pronounced systematic increase in the wall thickness of latewood tracheids outward from the pith at all levels. This pattern is associated with a consistent increase of wall thickness with decreasing height within each annual growth sheath: The rate of increase is rapid initially but declines with increasing age.

(b). Latewood Tracheid Lumen Diameter

There is a systematic decrease in the lumen diameter of the latewood tracheids outward from the pith. Within an annual growth sheath, the lumen diameter of latewood tracheids tends to remain relatively

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* At each level where these rings were visually distinguished: see Chapter 2 for a description of the sampling schedule.

Table 4.9: Parametric estimates (mean values, standard deviations, and between-tree range for 20 trees) of the cross-sectional dimensions of latewood tracheids in the third, seventh, and eleventh growth rings (from bark) at 6 height levels. Percentile heights refer to percentage of total tree height at the time of sampling.

Wood character	Height in tree	Ring number from bark					
		3		7		11	
		mean	s.d.	mean	s.d.	mean	s.d.
Latewood tracheid double-wall thickness (μ)	Breast height	19.2 (28.7 - 13.0)	3.1	17.5 (21.3 - 13.5)	2.2	14.7 (19.7 - 10.3)	2.4
	10%	18.7 (24.8 - 13.0)	2.8	17.4 (22.1 - 10.1)	2.7	14.5 (18.9 - 9.1)	3.2
	20%	18.4 (21.2 - 13.9)	2.0	16.6 (23.7 - 10.5)	3.0	12.0 (17.1 - 7.8)	2.6
	40%	16.1 (20.8 - 12.3)	2.4	14.0 (19.9 - 9.8)	2.8		
	60%	14.0 (18.5 - 8.9)	2.7				
	80%	9.8 (13.1 - 7.2)	1.8				
Latewood tracheid lumen diameter (μ)	Breast height	18.0 (35.8 - 9.1)	6.1	19.1 (25.7 - 11.2)	4.4	23.6 (41.4 - 14.9)	7.1
	10%	17.4 (26.7 - 9.4)	4.8	18.5 (31.6 - 10.7)	6.3	23.9 (39.8 - 13.3)	7.5
	20%	18.5 (28.5 - 9.8)	5.6	20.1 (36.6 - 12.8)	6.2	28.5 (40.9 - 12.6)	8.4
	40%	21.9 (44.3 - 10.6)	8.9	23.0 (39.8 - 11.9)	6.7		
	60%	22.7 (40.1 - 12.8)	6.9				
	80%	23.2 (33.4 - 16.0)	4.6				
Latewood tracheid diameter (μ)	Breast height	37.2 (53.9 - 26.0)	7.0	36.6 (43.4 - 30.0)	3.6	38.3 (51.8 - 30.9)	5.4
	10%	36.0 (48.8 - 25.5)	5.8	35.9 (46.1 - 28.0)	5.9	38.4 (51.7 - 30.1)	6.1
	20%	36.8 (47.7 - 28.8)	5.1	36.8 (47.1 - 30.1)	5.0	40.5 (51.9 - 26.7)	6.9
	40%	37.9 (56.6 - 28.8)	7.7	37.0 (50.5 - 28.4)	5.2		
	60%	36.7 (52.8 - 29.9)	5.5				
	80%	33.0 (40.6 - 24.9)	4.5				

constant in the lower sheath, and then to increase systematically with height. There is a high degree of between-tree variation (see Figure 4.11), much of which is related to tree vigour: The latewood tracheids of the more vigorous trees tend to have wider lumens (as noted in subsection 4.3.21.).

c). Latewood Tracheid Diameter

The variation in the overall diameter of the latewood tracheids is poorly defined. Tracheid width decreases outwards from the innermost rings in the lower bole, then remains relatively constant. The width of the latewood tracheids remains almost constant with height within each growth sheath.

Because of the sampling intensity, the pattern of variation of the anatomical characteristics with age is more comprehensively described in the oblique series, particularly in the outer ring (ring 3 from bark — see previous sub-section).

The rate of increase of radial double-wall thickness of the latewood tracheids with age is rapid initially (in the wood formed in close proximity to the living crown) but declines steadily with age. An essentially similar pattern of variation with age of radial double-wall thickness of the latewood tracheids was described (in the horizontal series) by Lantican [1972] in 10 30-year old trees of *Pinus caribaea* from a natural stand at Mt. Pine Ridge, British Honduras.

The quadratic trend of decrease with age in the radial lumen width of latewood tracheids (most comprehensively described in the oblique series) is similar to the pattern observed (in the horizontal series) by Lantican [1972]. Total radial width of latewood tracheids was independent of age: A finding consistent with that of Lantican [1972].

.2. Radial Cross-Sectional Dimensions of the Earlywood Tracheids

a). Earlywood Tracheid Double-Wall Thickness

There is a systematic increase of wall thickness of the earlywood tracheids outward from the pith at each height level. This pattern is reflected in the associated consistent decrease of wall thickness with height within each annual growth sheath. The variation of

Table 4.10: Parametric estimates (mean values, standard deviations, and between-tree range for 20 trees) of the C.S. dimensions of earlywood tracheids in the third, seventh, and eleventh growth rings (from bark) at 6 height levels.

Wood character	Height in tree	Ring number from bark: 3 mean	3 s.d.	7 mean	7 s.d.	11 mean	11 s.d.
Earlywood tracheid double-wall thickness (μ)	Breast height	10.3 (17.1 - 7.7)	2.1	9.1 (11.5 - 7.5)	1.0	8.4 (10.7 - 6.3)	1.0
	10%	9.4 (11.4 - 7.8)	1.4	8.9 (10.4 - 6.3)	1.1	8.2 (10.9 - 5.9)	1.2
	20%	9.2 (11.7 - 7.0)	1.3	8.1 (10.1 - 6.2)	1.1	7.7 (9.1 - 6.5)	.94
	40%	8.8 (12.6 - 7.3)	1.3	7.9 (10.1 - 6.7)	.87		
	60%	8.3 (10.4 - 6.8)	.91				
	80%	7.6 (10.0 - 5.6)	1.1				
Earlywood tracheid lumen diameter (μ)	Breast height	50.1 (63.2 - 32.6)	6.6	47.2 (64.5 - 35.2)	7.2	47.2 (60.3 - 38.7)	5.4
	10%	51.8 (59.3 - 40.5)	6.2	47.8 (58.8 - 32.5)	7.6	49.7 (61.5 - 36.3)	6.4
	20%	53.2 (66.9 - 43.2)	6.7	49.6 (58.1 - 39.8)	5.2	46.8 (63.9 - 38.8)	6.1
	40%	51.8 (66.8 - 40.9)	5.6	46.8 (58.4 - 35.1)	5.3		
	60%	50.3 (64.5 - 39.0)	6.2				
	80%	40.7 (53.8 - 30.0)	5.6				
Earlywood tracheid diameter (μ)	Breast height	60.4 (73.7 - 42.6)	6.9	56.2 (74.5 - 45.1)	7.4	55.6 (69.4 - 47.9)	5.0
	10%	61.2 (70.5 - 48.5)	6.7	56.7 (68.1 - 42.6)	7.4	57.9 (69.5 - 43.4)	6.6
	20%	62.3 (77.9 - 51.5)	7.1	57.7 (67.3 - 46.3)	5.3	54.5 (72.8 - 45.9)	6.4
	40%	60.6 (78.3 - 49.9)	6.3	54.7 (68.5 - 43.0)	5.5		
	60%	58.6 (74.8 - 46.7)	6.8				
	80%	48.3 (63.8 - 37.8)	6.3				

wall thickness with age in either sequence (horizontal or oblique) is more pronounced in the latewood than in the earlywood cells.

(b). Earlywood Tracheid Lumen Width

The lumen diameter of the earlywood tracheids is lowest in wood formed in the immediate vicinity of the live crown (see innermost rings at 20% and 40% and at 80% of total height), and appears to remain relatively stable with increasing age from the pith. Although the change in lumen diameter is of a relatively low order, there is a consistent pattern of variation within the oblique series (i.e., within each annual growth sheath): Lumen diameter increases with height to a maximum value and then decreases. The quadratic trend of variation of earlywood tracheid lumen diameter with age, evident in the oblique series, may be obscured in the horizontal series by the low sampling intensity.

There is a large element of between-tree variation (Figure 4.11) which is associated, to some extent, with tree vigour : The earlywood tracheids of the larger trees tend to have wider lumens (as noted in subsection 4.3.21.2.).

(c). Earlywood Tracheid Diameter

There is a general low-order increase in earlywood tracheid diameter outward from the pith. A quadratic trend of variation of cell diameter with height within the oblique series, generally similar to that of lumen diameter, is evident; i.e., with increasing height within an annual growth sheath, earlywood cell diameter increases to a maximum value and then decreases.

The general increase with age of the radial double-wall thickness of earlywood tracheids is consistent with the quadratic pattern of change demonstrated in 30-year old trees of *Pinus caribaea* from Mt. Pine Ridge [Lantican, 1972]. In the material of the present study the rate of change of wall thickness with age shows a less pronounced variation over the age range, although the increase initially (i.e., in wood formed in close proximity to the living crown – see oblique series; Table 4.10) tends to be greatest. In the younger material of the present study wall thickness does not appear to have reached a peak value (attained between rings 14 and 20 in the material studied by Lantican).

The quadratic pattern of increase of both radial lumen and cell width with age (most comprehensively described in the oblique series of ring 3 from bark — Table 4.10); rapid initially, then increasing relatively slowly with age to a peak value, is in agreement with the findings of Lantican [1972].

4.3.3. THE SYSTEMATIC VARIATION OF TRACHEID LENGTH WITHIN THE STEM

Parametric estimates of tracheid length in the earlywood of the third, seventh, and eleventh growth rings from the bark (see sampling schedule in Chapter 2) at six height levels are presented in Table 4.11. The variation of the average value of tracheid length within both the horizontal and oblique series is apparent in the tabular presentation.

Table 4.11: Parametric estimates (mean values, standard deviations, and between-tree range (in brackets) for the 10 trees of sub-plot A) of the length of the earlywood tracheids in the third, seventh, and eleventh (from bark) growth rings at 6 height levels.

Height in tree	Ring number from bark					
	3		7		11	
	mean	s.d.	mean	s.d.	mean	s.d.
Breast height	5.1 (6.0 - 4.4)	0.49	4.4 (4.9 - 3.2)	0.49	3.9 (4.3 - 3.4)	0.31
10%	5.3 (5.7 - 4.6)	0.33	4.7 (5.1 - 4.3)	0.24	4.0 (4.7 - 3.3)	0.38
20%	5.3 (5.6 - 5.1)	0.16	4.6 (5.0 - 4.4)	0.20	3.5 (4.0 - 2.9)	0.29
40%	5.1 (5.6 - 4.5)	0.35	4.2 (4.5 - 3.8)	0.25		
60%	4.6 (5.1 - 4.2)	0.27				
80%	3.4 (4.2 - 2.5)	0.54				

There is a pronounced systematic increase in tracheid length outward from the pith at each height level.

Within an annual growth sheath there is a quadratic trend of variation of tracheid length with height: Tracheid length increases with height to a maximum value and then decreases progressively towards the stem apex. The maximum tracheid length occurs in the lower stem; well below the region of the living crown. For example, in the third (from bark) ring the maximum tracheid length occurs between 10% and 20% of tree height at the time of sampling. The average disc values of tracheid length over the height range (breast height to 80%) are presented in Table 4.15.

There is a considerable range of between-tree variation of tracheid length (Table 4.11). Differences between whole-tree estimates are presented in sub-section 4.4 (Table 4.15).

The systematic variation within trees of tracheid length accords with Sanio's laws [Sanio, 1872] ; viz., tracheid length increases across the stem, and increases upwards in the stem to a maximum value then progressively decreases towards the stem apex. This general pattern of variation of tracheid length is commonly observed in gymnosperms [see extensive reviews of Spurr, Hyvärinen, 1954; Dinwoodie, 1961], but the literature contains numerous reports of differing patterns of variation outward from the pith in a wide range of species.

Generally similar patterns of variation of tracheid length within stems of tropical conifers have been reported recently; e.g., in *Pinus kesiya* [Burley, Andrew, 1970], *P. merkusii* [Andrew, Burley, 1973], and in 12-year old *P. caribaea* var. *caribaea* [Burley, Hughes, Lamb, 1971]. A linear increase in tracheid length from pith to bark was observed in 10-year old plantation-grown *P. caribaea* var. *hondurensis* from Jamaica [Brown, 1969, 1973; Burley *et al.*, 1973].

Lantican [1972] demonstrated a quadratic trend of increase of tracheid length with age from the pith in 30-year old trees of *P. caribaea* from a natural stand at Mt. Pine Ridge, British Honduras. Tracheid length increased rapidly from the pith to about ring 11 and attained a peak value between rings 14 and 20, then decreased slowly. This quadratic trend is consistent with the quadratic pattern of increase of tracheid length with age demonstrated in the oblique series (i.e.,

with decreasing height within an annual growth sheath) in the present study (Table 4.11). The attainment of a peak value of tracheid length with age was not found in the younger (10-year old) plantation-grown trees of *P. caribaea* var. *hondurensis* examined in other studies [e.g. Brown, 1969; Burley *et al.*, 1971].

4.4 THE EFFECT OF SAMPLE HEIGHT UPON THE ESTIMATE OF WHOLE-TREE VALUES OF WOOD CHARACTERS

The systematic variation of wood characters within a stem affects the accuracy with which the whole-tree values of these characters may be estimated from a sample taken at a given level within the stem. Determination of the relationship between the height at which a sample is taken and the accuracy of estimate of the whole-tree value is a prerequisite of the development of small scale non-destructive sampling schemes. Such sampling schemes may yield data from which valid between-tree comparisons can be made.

The degree to which a pith-to-bark sample at various height levels (discs) is representative of the whole-tree value has been examined by correlation analysis. Linear regression analysis is used to indicate the accuracy of prediction of whole-tree values from disc values at the breast and percentile levels.

Estimates of wood character parameters for each level within trees and for whole trees were derived as both arithmetic averages and weighted averages. Bias of the arithmetic average has been discussed by Stokes (1921).

The arithmetic procedures for computing the arithmetic and weighted disc average values of the wood characters were as follows:

(i) Arithmetic Average Values

(a) Arithmetic Disc Average Value, x_{DA}

$$x_{DA} = \frac{\sum_{i=1}^{n} x_i}{n},$$

where,

x_i is the value of variable x at ring i,

n is the number of rings in the disc.

(b) Arithmetic Whole-Tree Average Value, x_{TA}

The arithmetic whole-tree average value of a variable, x_{TA}, was calculated as the summation of the disc values divided by the number of discs. Thus,

$$x_{TA} = \frac{\sum_{k=1}^{q} (x_{DA})_k}{q},$$

where q is the number of discs.

(ii) Weighted Average Values

(a) Weighted Disc Average Value, x_{DW}

To calculate the weighted disc average value of a variable the measured ring value was assumed to represent the value within an annular area with radii corresponding with the inner and outer radii of the annual ring. Then,

$$x_{DW} = \frac{\sum_{i=1}^{n} (x_i \cdot a_i)}{a_T},$$

where,

x_i is the value of variable x at ring i,

a_i is the annular area corresponding to ring i,

a_T is the total area of the disc.

The measured value of a variable in each ring is thus weighted roughly in proportion to the area of disc that the ring occupies.

(b) Weighted Whole-Tree Average Value, x_{TW}

The weighted disc average value, x_{DW}, of a variable is assumed to represent the value of that variable in the portion of the stem bounded by the mid-points between discs. Then,

$$x_{TW} = \frac{\sum_{k=1}^{q} [(x_{DW})_k - v_k]}{v_T},$$

where,

q is the number of discs,

v_k is the volume of stem represented by the disc value,

v_T is the total volume of the stem.

The weighted disc average value of a variable is thus weighted in proportion to that volume of the stem which the disc value is assumed to represent.

For between-tree comparison of a wood character the following criteria are important:

(a) The degree to which the value of a variable estimated from a sample taken at a particular height represents the whole-tree value. The correlations between the disc and whole-tree values provide an estimate of the sample representativeness. Product-moment correlation coefficients, together with their standard errors and significance, are presented. The greater the value of the correlation coefficient and the higher the degree of significance, the more representative is the pith-to-bark sample of the whole-tree value.

(b) The sample error associated with the prediction of the whole-tree value from disc values at the various height levels. A linear relationship between disc values and whole-tree values is assumed: This assumption is not seriously violated by the data, particularly when considering the more representative samples. The sample error is indicated by the standard errors of the estimate of regressions, and the statistical significance of both the regression lines and regression coefficients.

(c) Errors associated with the measurement of the variable (considered in Chapter 3).

A comparison of the whole-tree values with the errors of (b) and (c) may indicate the usefulness of a particular variable for between-tree comparison. Between-tree comparison of a variable is of little use if the sampling and measurement errors approach or exceed the between-tree differences. The implications are particularly important in selection of characters for breeding.

The implications of sample representativeness for the design of small scale non-destructive sampling schemes will necessarily be restricted in practice by the convenience of sampling the standing tree at the representative height.

(a) Wood Density

The parameters presented in Tables 4.12 a - e are calculated from the densitometric measures of all the growth rings in each of 6 discs from 20 trees.

Ring Maximum Density (Table 4.12a)

The correlation of each of the disc values with the whole-tree values is highly significant for both arithmetic and weighted estimates, indicating that a pith-to-bark sample taken at any given level between breast height and 80% of total tree height may be taken to represent the whole-tree value for between-tree comparison. The magnitude of the correlation coefficient is less at 60% and 80% of tree height, indicating that discs taken below 60% of tree height are more representative of whole-tree values.

Weighted whole-tree average values range from .618 to .961 or 43% of the mean value (.798). The standard error of estimate of the regression of the weighted whole-tree values on the disc values at 20% of tree height is .007 g/cc or less than 1% of the mean.

Ring Minimum Density (Table 4.12b)

Weighted whole-tree average values of ring minimum density range from .315 to .417 or 29% of the mean value (.347), while the

Tables 4.12 a - e: Parametric estimates (20 trees) of whole-tree and disc values of (a) Maximum density; (b) Minimum density; (c) Mean density; (d) Density range; and (e) Latewood percentage; their inter-correlation, and the regression of whole-tree values (y) on disc values (x).

The notations used are explained in the text: Thus, e.g., $\bar{x}_{DA}$ is the mean of the arithmetic disc average value of a variable; $\bar{x}_{DW}$ the mean weighted value.

Coefficients of correlation between whole-tree and disc values, both

arithmetic ($r_{x_{DA.TA}}$) and weighted ($r_{x_{DW.TW}}$),

their standard errors (s.e.), and significance are presented.

Table 4.12a: Ring maximum density (20 trees).

Whole tree value:	mean	s.d.	s.e.
(i) arithmetic (x_{TA})	.738	.085	
(ii) weighted (x_{TW})	.798	.096	.022

Height in tree	$\bar{x}_{DA}$	s.d.	$\bar{x}_{DW}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	r $x_{DW} \cdot x_{TW}$	s.e.
Breast height	.804	.089	.859	.092	.935 ***	.083	.929 ***	.087
10%	.809	.097	.852	.103	.897 ***	.104	.892 ***	.107
20%	.764	.095	.811	.107	.926 ***	.089	.948 ***	.075
40%	.706	.094	.757	.104	.925 ***	.090	.954 ***	.070
60%	.685	.097	.749	.123	.850 ***	.124	.842 ***	.127
80%	.662	.107	.725	.131	.787 ***	.145	.739 ***	.159

Regression analysis
whole tree value (y), disc values (x)

Height in tree	Regression line			Regression coefficient
	equation	s.e.	F	s.e.
(a) Arithmetic values				
Breast height	y = .02 + .89 x	.007	126.2 ***	.019 ***
10%	y = .10 + .79 x	.009	74.2 ***	.022 ***
20%	y = .10 + .84 x	.008	109.1 ***	.019 ***
40%	y = .14 + .84 x	.008	106.6 ***	.019 ***
60%	y = .22 + .75 x	.011	46.9 ***	.026 ***
80%	y = .32 + .63 x	.013	29.3 ***	.027 ***
(b) Weighted values				
Breast height	y = -.03 + .97 x	.009	113.7 ***	.021 ***
10%	y = .08 + .84 x	.011	69.9 ***	.024 ***
20%	y = .11 + .85 x	.007	160.3 ***	.016 ***
40%	y = .13 + .88 x	.007	183.9 ***	.015 ***
60%	y = .30 + .66 x	.013	44.0 ***	.023 ***
80%	y = .40 + .54 x	.016	21.6 ***	.028 ***

Table 4.12b: Ring minimum density (20 trees).

Whole tree value	mean	s.d.	s.e.
(i) Arithmetic (x_{TA})	.346	.024	
(ii) Weighted (x_{TW})	.347	.027	.006

Height in tree	$\bar{x}_{DA}$	s.d.	$\bar{x}_{DW}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	r $x_{DW} \cdot x_{TW}$	s.e.
Breast height	.359	.031	.364	.031	.965 ***	.062	.965 ***	.062
10%	.355	.034	.357	.033	.941 ***	.079	.945 ***	.077
20%	.343	.031	.344	.029	.933 ***	.085	.949 ***	.074
40%	.340	.027	.340	.027	.977 ***	.050	.982 ***	.044
60%	.337	.022	.340	.027	.856 ***	.122	.874 ***	.115
80%	.344	.020	.342	.020	.535 *	.199	.590 **	.190

Regression analysis
whole tree value (y), disc values (x)

Height in tree	Regression line			Regression coefficient
	equation	s.e.	F	s.e.
(a) Arithmetic values				
Breast height	y = .07 + .76 x	.002	244.7 ***	.011 ***
10%	y = .10 + .68 x	.002	140.3 ***	.014 ***
20%	y = .09 + .75 x	.002	121.1 ***	.016 ***
40%	y = .05 + .88 x	.001	381.0 ***	.011 ***
60%	y = .03 + .95 x	.003	49.5 ***	.032 ***
80%	y = .12 + .65 x	.005	7.2 *	.057 ***
(b) Weighted values				
Breast height	y = .04 + .85 x	.002	242.3 ***	.013 ***
10%	y = .07 + .78 x	.002	149.0 ***	.015 ***
20%	y = .05 + .87 x	.002	164.7 ***	.016 ***
40%	y = .01 + .98x	.001	492.2 ***	.010 ***
60%	y = .05 + .87 x	.003	58.2 ***	.027 ***
80%	y = .07 + .81 x	.005	9.6 **	.061 ***

standard error of estimate (.002) at 20% of tree height is less than 1% of the mean. The values estimated for each height level from breast height to 60% of tree height faithfully represent the whole tree estimates.

Ring Mean Density (Table 4.12c)

As for the values of ring maximum and minimum density, the range of estimate of weighted whole-tree mean density between trees (.414 to .594) is high (36%) in relation to the mean value (.495), indicating substantial phenotypic differences between trees. The sample error (less than 1% of the mean value at 20% of tree height) is again low. A faithful estimate of the whole-tree value is obtained from each of the height levels, but the magnitude of the correlation coefficient is lower above 40% of tree height.

Ring Density Range (Table 4.12d)

The weighted whole-tree average values of the intra-incremental density range range from .303 to .601 which is 66% of the mean whole-tree value (.450), while the sample error (.007) at 20% of tree height is less than 2% of the mean. The values estimated at each level from breast height to 80% of tree height faithfully represent the whole-tree estimates, although the levels below 60% are more representative.

Latewood Percentage (Table 4.12e)

Very large phenotypic differences between trees are evident. Weighted whole-tree average values range from 17.28% to 64.32% or 128% of the mean whole-tree value (36.81%). The sample error at 20% of tree height (.777%) is negligible (<< 1%). Estimates from discs to 60% of tree height are each highly representative of the whole-tree values.

For each of the densitometric characters, the disc average estimate at 20% of tree height very closely approximates the whole-tree average value. Average values of each character estimated from measures of discs taken below and above 20% of tree height overestimate and underestimate respectively the whole-tree average value of the character. Average estimates derived from measures of discs taken at any given level

Table 4.12c: Ring mean density (20 trees).

Whole tree value	mean	s.d.	s.e.
(i) Arithmetic (x_{TA})	.478	.040	
(ii) Weighted (x_{TW})	.495	.044	.010

Height in tree	$\bar{x}_{DA}$	s.d.	$\bar{x}_{DW}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	r $x_{DW} \cdot x_{TW}$	s.e.
Breast height	.518	.044	.538	.041	.904 ***	.101	.881 ***	.112
10%	.514	.051	.529	.050	.919 ***	.093	.877 ***	.113
20%	.487	.054	.502	.055	.933 ***	.085	.934 ***	.084
40%	.461	.053	.472	.053	.957 ***	.068	.940 ***	.080
60%	.442	.038	.458	.046	.804 ***	.140	.803 ***	.140
80%	.445	.033	.457	.037	.702 ***	.168	.677 **	.174

Regression analysis
whole tree value (y), disc values (x)

Height in tree	Regression line			Regression coefficient
	equation	s.e.	F	s.e.
(a) Arithmetic values				
Breast height	y = .05 + .83 x	.004	80.1 ***	.022 ***
10%	y = .11 + .72 x	.004	97.6 ***	.017 ***
20%	y = .14 + .70 x	.003	121.1 ***	.015 ***
40%	y = .14 + .73 x	.003	196.5 ***	.012 ***
60%	y = .10 + .85 x	.006	32.9 ***	.035 ***
80%	y = .10 + .86 x	.007	17.4 ***	.048 ***
(b) Weighted values				
Breast height	y = -.01 + .94 x	.004	62.3 ***	.028 ***
10%	y = .09 + .77 x	.005	59.9 ***	.023 ***
20%	y = .12 + .74 x	.004	123.2 ***	.016 ***
40%	y = .13 + .78 x	.004	136.9 ***	.016 ***
60%	y = .14 + .77 x	.006	32.8 ***	.032 ***
80%	y = .12 + .81 x	.008	15.2 ***	.049 ***

Table 4.12d: Ring density range (20 trees).

Whole tree value	mean	s.d.	s.e.
(i) Arithmetic (x_{TA})	.392	.075	
(ii) Weighted (x_{TW})	.450	.087	

Height in tree	$\overline{x}_{DA}$	s.d.	$\overline{x}_{DW}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	r $x_{DW} \cdot x_{TW}$	s.e.
Breast height	.445	.079	.494	.087	.925 ***	.089	.924 ***	.090
10%	.454	.086	.494	.093	.901 ***	.102	.904 ***	.101
20%	.421	.081	.467	.096	.911 ***	.097	.941 ***	.080
40%	.366	.083	.417	.096	.904 ***	.101	.950 ***	.074
60%	.348	.088	.409	.111	.838 ***	.128	.840 ***	.128
80%	.318	.097	.384	.120	.784 ***	.146	.713 ***	.165

Regression analysis
whole tree value (y), disc values (x)

Height in tree	Regression line			Regression coefficient
	equation	s.e.	F	s.e.
(a) Arithmetic values				
Breast height	y = 0 + .87 x	.007	107.4 ***	.020 ***
10%	y = .03 + .79 x	.008	77.9 ***	.021 ***
20%	y = .04 + .84 x	.007	87.9 ***	.021 ***
40%	y = .09 + .81 x	.008	80.6 ***	.021 ***
60%	y = .14 + .72 x	.010	42.6 ***	.026 ***
80%	y = .20 + .60 x	.011	28.6 ***	.027 ***
(b) Weighted values				
Breast height	y = -.01 + .93 x	.008	105.3 ***	.021 ***
10%	y = .03 + .85 x	.009	80.4 ***	.022 ***
20%	y = .05 + .85 x	.007	138.3 ***	.017 ***
40%	y = .09 + .87 x	.007	167.0 ***	.016 ***
60%	y = .18 + .66 x	.011	43.0 ***	.024 ***
80%	y = .25 + .52 x	.015	18.7 ***	.028 ***

Table 4.12e: Latewood percentage (20 trees).

Whole tree value	mean	s.d.	s.e.
(i) Arithmetic (x_{TA})	31.50	10.97	
(ii) Weighted (x_{TW})	36.81	11.68	2.612

Height in tree	$\bar{x}_{DA}$	s.d.	$\bar{x}_{DW}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	r $x_{DW} \cdot x_{TW}$	s.e.
Breast height	43.66	12.95	49.02	12.34	.962 ***	.064	.951 ***	.073
10%	41.16	14.32	45.09	13.93	.942 ***	.079	.914 ***	.096
20%	36.18	13.21	39.69	12.62	.955 ***	.070	.962 ***	.065
40%	29.09	12.95	31.38	12.96	.960 ***	.066	.963 ***	.064
60%	20.60	11.15	24.38	12.50	.855 ***	.122	.839 ***	.128
80%	18.33	7.85	22.15	9.17	.672 **	.175	.660 **	.177

Regression analysis
whole tree value (y), disc values (x)

Height in tree	Regression line			Regression coefficient
	equation	s.e.	F	s.e.
(a) Arithmetic values				
Breast height	y = -4.08 + .82 x	.722	225.8 ***	.013 ***
10%	y = 1.80 + .72 x	.890	142.2 ***	.014 ***
20%	y = 2.80 + .79 x	.784	2086.2 ***	.014 ***
40%	y = 7.86 + .81 x	.748	209.2 ***	.013 ***
60%	y = 14.18 + .84 x	1.377	48.9 ***	.028 ***
80%	y = 14.29 + .94 x	1.968	14.8 **	.058 ***
(b) Weighted values				
Breast height	y = -7.30 + .90 x	.875	170.1 ***	.016 ***
10%	y = 2.27 + .77 x	1.150	90.8 ***	.019 ***
20%	y = 1.50 + .89 x	.777	220.4 ***	.014 ***
40%	y = 9.58 + .87 x	.763	229.2 ***	.014 ***
60%	y = 17.71 + .78 x	1.540	42.7 ***	.028 ***
80%	y = 18.19 + .84 x	2.125	13.9 **	.053 ***

from breast height to 60% of tree height are, however, representative of whole-tree values for the purpose of between-tree comparison.

(b) Tracheid Cross-Sectional Dimensions

The parameters presented in Tables 4.13 a - f, were calculated from measures of the 3rd, 7th, and 11th rings from the bark in each of 5 discs in which they occurred. In most of the 20 trees measured, all 3 rings occurred at breast height, 10% and 20% of tree height, rings 3 and 7 at 40%, and ring 3 only at 60% of tree height.

For each of the variables measured, the correlation of each of the disc values with the whole-tree values is highly significant, indicating that a pith-to-bark sample taken at any given level between breast height and 60% of total tree height may be taken to represent the estimate of the whole-tree value for between-tree comparison.

There is a high degree of phenotypic variation between trees (Table 4.14) with each of the characters. In each case the sample error is very small in relation to the between-tree differences.

(c) Tracheid Length

The parameters presented in Table 4.15 were calculated from measures of the length of the earlywood tracheids in 10 trees (sub-plot A) using rings 3, 7, and 11 as for the measure of cell cross-section dimensions.

Arithmetic whole-tree average values range from 4.240 mm - 4.847 mm or 13% of the mean whole-tree value (4.571 mm). The phenotypic differences between trees is considerably less for tracheid length than for tracheid cross-sectional dimensions. Sample error ranges from 0.6% of the mean (breast height) to 1.5% (20% of tree height). Correlations between disc and whole-tree values range from very highly significant ($p < .001$) at breast height to not significant at 20% of tree height.

Tables 4.13 a - f: Parametric estimates (20 trees) of whole-tree (above) and disc (mean = $\bar{x}_{DA}$; standard deviation = s.d.) arithmetic values of: Latewood tracheid double-wall thickness, lumen width, and cell diameter (tables a - c, repsectively); and earlywood tracheid double-wall thickness, lumen width, and cell diameter (tables d - f, respectively); their inter-correlation, and the regression of whole-tree values (y) on disc values (x).

Coefficients of correlation between whole-tree and disc values

$$(r_{x_{DA.TA}}),$$

with their standard errors (s.e.) and significance are presented.

Table 4.13a: Latewood cell double-wall thickness (μ).

Whole-tree arithmetic value:

mean	s.d.	s.e.
15.73	1.82	0.407

Height in tree	$\bar{x}_{DA}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	Regression line			Regression coefficient
					equation	s.e.	F	s.e.
Breast height	17.11	1.82	.650 **	.179	y = 4.58 + .65 x	.335	13.2 **	.042 ***
10%	16.84	2.11	.910 ***	.097	y = 2.53 + .78 x	.182	87.2 ***	.020 ***
20%	15.65	1.85	.873 ***	.115	y = 2.27 + .86 x	.215	57.6 ***	.027 ***
40%	15.04	2.28	.908 ***	.099	y = 4.82 + .73 x	.185	84.4 ***	.019 ***
60%	14.03	2.69	.860 ***	.120	y = 7.58 + .58 x	.225	51.2 ***	.019 ***

Table 4.13b: Latewood cell lumen width (μ).

Whole-tree arithmetic value:

mean	s.d.	s.e.
21.53	5.12	1.145

Height in tree	$\bar{x}_{DA}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	Regression line			Regression coefficient
					equation	s.e.	F	s.e.
Breast height	20.25	4.81	.909 ***	.098	y = 1.94 + .97 x	.517	85.5 ***	.025 ***
10%	19.93	5.08	.868 ***	.117	y = 4.10 + .87 x	.616	54.8 ***	.028 ***
20%	22.37	5.11	.921 ***	.092	y = .89 + .92 x	.482	101.3 ***	.022 ***
40%	22.43	6.37	.953 ***	.071	y = 4.35 + .77 x	.376	177.7 ***	.014 ***
60%	22.67	6.86	.880 ***	.112	y = 6.65 + .66 x	.558	61.9 ***	.020 ***

Table 4.13c: Latewood cell diameter (μ).

Whole-tree arithmetic value:

mean	s.d.	s.e.
32.27	4.10	0.917

Breast height	$\bar{x}_{DA}$	s.d.	$r_{x_{FA} \cdot x_{TA}}$	s.e.	Regression line			Regression coefficient
					equation	s.e.	F	s.e.
Breast height	37.38	4.28	.938 ***	.082	y = 3.63 + .90 x	.344	131.9 ***	.018 ***
10%	36.76	4.82	.827 ***	.133	y = 11.39 + .70 x	.559	38.9 ***	.027 ***
20%	38.03	4.10	.858 ***	.121	y = 4.57 + .86 x	.510	50.3 ***	.029 ***
40%	37.48	4.84	.923 ***	.091	y = 7.94 + .78 x	.382	103.5 ***	.018 ***
60%	36.70	5.51	.823 ***	.134	y = 14.77 + .61 x	.564	37.9 ***	.023 ***

Table 4.13d: Earlywood cell double-wall thickness (μ).

Whole-tree arithmetic value:

mean	s.d.	s.e.
8.61	0.85	0.190

Height in tree	$\bar{x}_{DA}$	s.d.	$r_{x_{DA} \cdot x_{TA}}$	s.e.	Regression line			Regression coefficient
					equation	s.e.	F	s.e.
Breast height	9.24	1.10	.733 ***	.160	y = 3.35 + .57 x	.140	20.8 ***	.029 ***
10%	8.82	1.03	.848 ***	.125	y = 2.44 + .70 x	.109	46.0 ***	.024 ***
20%	8.33	.94	.927 ***	.089	y = 1.65 + .84 x	.078	109.2 ***	.019 ***
40%	8.37	.97	.916 ***	.095	y = 1.87 + .81 x	.083	93.4 ***	.020 ***
60%	8.29	.91	.901 ***	.102	y = 1.61 + .85 x	.090	77.3 ***	.023 ***

Table 4.13e: Earlywood cell lumen width (μ).

Whole-tree arithmetic value:

mean	s.d.	s.e.
49.48	4.77	1.067

Height in tree	$\bar{x}_{DA}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	Regression line			Regression coefficient
					equation	s.e.	F	s.e.
Breast height	48.16	5.68	.947 ***	.076	y = 11.18 + .80 x	.372	155.3 ***	.015 ***
10%	49.76	5.96	.852 ***	.123	y = 15.56 + .68 x	.604	47.7 ***	.023 ***
20%	49.86	4.91	.825 ***	.133	y = 9.51 + .80 x	.653	38.3 ***	.031 ***
40%	49.26	4.70	.860 ***	.120	y = 6.48 + .87 x	.589	51.3 ***	.029 ***
60%	50.34	6.15	.861 ***	.120	y = 15.87 + .67 x	.586	51.8 ***	.022 ***

Table 4.13f: Earlywood cell diameter (μ).

Whole-tree arithmetic value:

mean	s.d.	s.e.
58.08	5.09	1.138

Height in tree	$\bar{x}_{DA}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	Regression line			Regression coefficient
					equation	s.e.	F	s.e.
Breast height	57.41	5.79	.937 ***	.083	y = 10.81 + .82 x	.432	128.8 ***	.017 ***
10%	58.58	6.09	.846 ***	.126	y = 16.66 + .71 x	.658	45.2 ***	.025 ***
20%	58.19	5.21	.831 ***	.131	y = 10.81 + .81 x	.685	40.2 ***	.030 ***
40%	57.63	5.17	.872 ***	.115	y = 8.63 + .86x	.603	57.1 ***	.027 ***
60%	58.62	6.77	.892 ***	.106	y = 18.75 + .67x	.557	70.3 ***	.019 ***

Table 4.14: The between-tree range (20 trees) of the estimate of the arithmetic whole-tree average values of latewood and earlywood cross-sectional dimensions.

Wood character	Arithmetic whole-tree average value		Range as % of mean	Sample error (%)*
	range	mean		
Latewood cell wall thickness (μ)	12.24 - 18.21	15.73	38	1
Latewood cell lumen diameter (μ)	12.77 - 33.12	21.53	95	2
Latewood cell diameter	30.65 - 47.00	37.27	44	1
Earlywood cell wall thickness (μ)	7.11 - 10.48	8.61	39	1
Earlywood cell lumen diameter (μ)	39.94 - 62.37	49.48	45	1
Earlywood cell diameter	48.33 - 72.43	58.08	41	1

* s.e. of estimate of the regression of arithmetic whole-tree values on disc values at 20% of tree height.

Table 4.15: Parametric estimates of whole-tree (above) and disc (mean = $\bar{x}_{DA}$; standard deviation = s.d.) arithmetic values of earlywood tracheid length; their inter-correlation, and the regression of whole-tree values (y) on disc values (x).

Coefficients of correlation between whole-tree and disc values

$$(r_{x_{DA} \cdot TA}) ,$$

with their standard errors (s.e.) and significance are presented.

Whole-tree arithmetic value:

mean	s.d.	s.e.
4.571	.183	.041

Height in tree	$\bar{x}_{DA}$	s.d.	r $x_{DA} \cdot x_{TA}$	s.e.	Regression line			Regression coefficient
					equation	s.e.	F	s.e.
Breast height	4.453	.349	.897 ***	.157	y = 2.48 + .47 x	.030	32.8 ***	.029 ***
10%	4.658	.191	.712 *	.248	y = 1.41 + .68 x	.048	8.2 *	.084 ***
20%	4.467	.104	.119 NS	.351	y = 3.63 + .21 x	.068	0.1 NS	.218 NS
40%	4.643	.269	.851 **	.186	y = 1.89 + .58 x	.036	20.9 **	.045 ***
60%	4.631	.272	.818 **	.204	y = 2.03 + .55 x	.039	16.1 **	.048 ***

4.5. AN ESTIMATE OF THE EFFECTS UPON WOOD CHARACTERISTICS OF RADIAL GROWTH RATE AND POSITION WITHIN THE STEM

Systematic trends of covariation of many of the wood characters with position effects associated with height and age, and with growth rate have been identified. Patterns of variation with age and height are suggestive of response of the wood characteristics to distance of the site of wood formation from the active regions of the live crown. The causal influences underlying the systematic pattern of response of the wood characteristics are essentially physiological in nature. But, in the sense that they represent the sites of wood formation within polar gradients of physiological influence emanating from the active crown (and presumably the roots; cf., the little-known role of cytokinins), the position effects (age and height) may be regarded as exerting a direct causal influence upon the properties of the wood. Radial growth rate (measured as width of the annual rings) may have a direct causal effect upon the variation of other measured wood properties.

Where direct causal effects exist, or their existence can be implied by hypothesis, the variables may be classified as either "stimulus" (explanatory) or "response" (explained) characters, and the relationship estimated by correlation and regression analysis.

The correlations between the individual variables of each group (r_{yx}); between the independent (stimulus) variables and orthogonal linear combinations (principal components) of the dependent (response) variables (r_{zx}), and between the principal components of each group (r_{zw}), may be estimated.

An estimate of the combined effect of the stimulus characters (position effects, growth rate) upon each of the response characters is provided by the multiple regression of each dependent variable on the independent variables.

If it is assumed that the variation in the characteristics of the wood is at least in part a response to the influence of growth rate and the position effects associated with age and height (stimulus characters), then the relationship may be expressed in one or more meaningful linear equations of the type

$$\sum_{j=1}^{p} y_{ij}\, a_{j\ell} = \sum_{k=1}^{q} x_{ik}\, b_{k\ell} + \varepsilon_{i\ell}\,, \qquad (1)$$

$$i = 1, \ldots, n; \quad \ell = 1, \ldots, m\,,$$

where $a_{j\ell}$ and $b_{k\ell}$ are constants appropriate to the jth response character, kth stimulus character, and ℓth equation; $\varepsilon_{i\ell}$ is an error term for the ith observation (sample unit) and ℓth equation; p and q are the number of response and stimulus characters respectively; n is the number of observations; and m is the number of equations.

The convention of X (independent variable) and Y (dependent variable) is based upon regression analysis. The lower case y and x are standardised values corresponding with Y and X, e.g., $y_{ij} = (Y_{ij} - \bar{y}_j)/s_j$, where $\bar{y}_j$ and s_j are the mean and standard deviation of Y_{ij}. The x's and y's are normal variates that are linearly related.

The principal components

$$z_{i\ell} = \sum_{j=1}^{p} y_{ij}\, a_{j\ell}$$

produce a y-function comparable to the left hand side of equation (1). The a's in (1) are the elements of one of the eigenvectors of the matrix of inter-correlations among the response variables.

The b's (partial regression coefficients) in the x-function (right hand side of equation (1)) can be derived by multiple regression analysis, with z as dependent variable and the x's as independent variables.

A multiple regression analysis substituting the principal components of the stimulus variables, w_{ℓ}, as independent variables has also been attempted. This is appropriate in the later applications of this analytical technique (Section 4.7) involving soil and foliar nutrient levels as stimulus variables, since one would expect the characteristics of the wood to respond to complexes of inter-related environmental factors rather than to individual measurable factors (x's).

Although p equations (as many as there are "explained" wood characters) are necessary to account for all the sample information, the number of equations may be reduced to m (< p) by deleting the principal components (z's) with the smaller eigenvalues (Appendix I) with minimal discard of information.

The computations were facilitated by the use of a computer programme, "MULTIPAK", which was developed from a series of programmes written in FORTRAN IV by Professor R.M. Cassie, University of Auckland [Cassie, 1972], and modified to be compatible with a UNIVAC 1108 computing system.

The information contained in data set C (see Section 4.2; Table 4.2) has been examined to estimate the effects upon the variation of the wood characteristics (density features, proportion of latewood, and cell dimensions) of growth rate and of position associated with height in the stem and with age and radial distance from the pith.

The product-moment correlation coefficients, r_{yx}, for each response and stimulus character pair are presented in Table 4.16.

54 and 43 of the 65 coefficients are significant at the 5% and 1% level, respectively. This high level of significant inter-correlation of the stimulus and response variables is reflected in the moderate level of the multiple correlation coefficient, R, for response characters × (combined stimulus characters), which ranges from 0.47 (earlywood tracheid wall thickness) to 0.84 (tracheid length).

Table 4.16: Response characters × stimulus characters (p = 13 columns × q = 5 rows) correlation matrix.

Multiple correlation coefficients, R, for response characters × (combined stimulus characters) are listed.

For n = 128 observations the critical levels of r_{yx} are: 0.17 (.05)*; 0.23 (.01)**.

	1 DMAX	2 DMIN	3 DEN	4 DR	6 % LW	7 LWID	9 LWW	10 LWL	11 EWW	12 EWL	13 LWCD	14 EWCD	15 LFIB
x_1 ring age	26	35	29	20	18	-09	23	-24	21	19	-14	23	61
x_2 pith distance	61	22	54	62	43	45	61	-17	43	42	19	50	66
x_3 % tree height	-47	-23	-44	-47	-51	-42	-44	19	-29	-10	-06	-16	-23
x_4 height	-46	-26	-44	-44	-51	-38	-42	22	-29	-05	-01	-12	-22
x_5 ring width	-38	-68	-48	-27	-51	16	-31	54	-21	07	45	01	-57
R	.71	.75	.70	.68	.71	.61	.67	.56	.48	.47	.56	.53	.84

The correlation coefficients provide an index of affinity of each stimulus × response variable pair, but the correlations may arise as a result of response to direct causal effects and/or through co-response to a common influence. In this instance they are relatively poor estimates of the effect of individual stimulus variables upon the response variables because the pronounced systematic variation within trees of ring width and many of the densitometric characters and tracheid dimensions is approximately collinear with ring number. Because of this it is difficult to estimate the relative importance of radial position effects (ring number, or distance from pith) and growth rate (ring width), although it seems probable that the effect of growth rate is of minor significance except in the juvenile core of fast-, plantation-grown species [see Spurr, Hsiung, 1954; Dadswell, Nicholls, 1959; Goggans, 1961; Jeffers, 1966].

In contrast to the strong negative association of ring width with mean density ($r = -0.48$) (and other densitometric characters) and with tracheid length (-0.57) demonstrated in this study, Lantican [1972] found no significant correlation between ring width and either mean density or tracheid length in 30-year old trees of var. *hondurensis* from a natural stand in British Honduras.

The coefficients of determination, R^2, for the multiple regression of each response variable on the five stimulus variables, and the partial regression coefficients for these equations are presented in Table 4.17. The combined stimulus variables account for a considerable portion (roughly 50%) of the variation of each of the densitometric characters. Of the tracheid dimensions, the variation of tracheid length is most faithfully predicted ($R^2 = 0.71$) by the combined measures of height, radial position, and growth rate; between 31% and 45% of the variance of the latewood tracheid C.S. dimensions are accounted for; but the earlywood tracheid C.S. dimensions each are poorly predicted.

The factor loadings of each of the response variables on the first 5 principal components, z_{1-5}, are listed in Table 4.18a. The affinity of each variable with the main components is shown in Figure 4.15.

Table 4.17: Vectors of partial regression coefficients, b, for the equations of multiple regression for each independent (response) variable, y_{ℓ}, on the five dependent (stimulus) variables, x_{1-5}. The multiple correlation coefficients, R, and coefficients of determination, R^2, are listed.

	1 DMAX	2 DMIN	3 DEN	4 DR	6 % LW	7 LWID	9 LWW	10 LWL	11 EWW	12 EWL	13 LWCD	14 EWCD	15 LFIB
x_1 ring age	.33	.95	.46	.15	.68	-.05	.07	-.43	.38	-.23	-.47	-.13	.53
x_2 pith distance	.19	-.67	.05	.36	-.30	.42	.42	.27	.10	.58	.59	.58	.16
x_3 % tree height	-1.1	-1.2	-.57	-.96	-1.2	.03	-.85	.48	.07	-.82	.02	-.76	-1.27
x_4 height	.63	.41	-.01	.60	.28	-.36	.60	-.10	-.53	1.08	.28	.90	.90
x_5 ring width	-.15	-.30	-.16	-.10	-.12	.34	-.18	.35	.10	-.05	.31	-.02	-.36
R	.71	.75	.70	.68	.71	.61	.67	.56	.48	.47	.56	.53	.84
R^2	.50	.56	.49	.46	.50	.37	.45	.32	.23	.22	.31	.28	.71

Table 4.18: Eigenvalues, λ, and vectors, f, of standardised variation in (a) response characters, and (b) stimulus characters.

Table 4.18a

Principal component	z_1	z_2	z_3	z_4	z_5
Eigenvalue (λ)	6.31	2.47	1.47	0.89	0.69
Percentage of variance	49	19	11	7	5
Cumulative percentage	49	68	79	86	91
Variable					
1 DMAX	93	08	01	-21	-05
3 DEN	90	-21	16	-05	-13
4 DR	87	19	02	-32	-03
6 % LW	86	-29	21	03	-15
9 LWW	83	25	12	07	17
2 DMIN	66	-48	-07	43	-10
15 LFIB	61	21	-30	34	-53
7 LWID	61	02	63	-32	-01
11 EWW	59	10	26	52	48
14 EWCD	39	86	-25	05	12
12 EWL	26	88	-33	-07	00
13 LWCD	-35	58	65	20	-18
10 LWL	-74	35	48	13	-24

Table 4.18b

Principal component	w_1	w_2	w_3
Eigenvalue (λ)	2.43	1.69	0.82
Percentage of variance	49	34	17
Cumulative percentage	49	83	100
Variable			
2 pith distance	44	72	53
1 ring age	-35	93	03
5 ring width	-41	-54	73
3 tree height (%)	-99	11	-09
4 height	-99	11	01

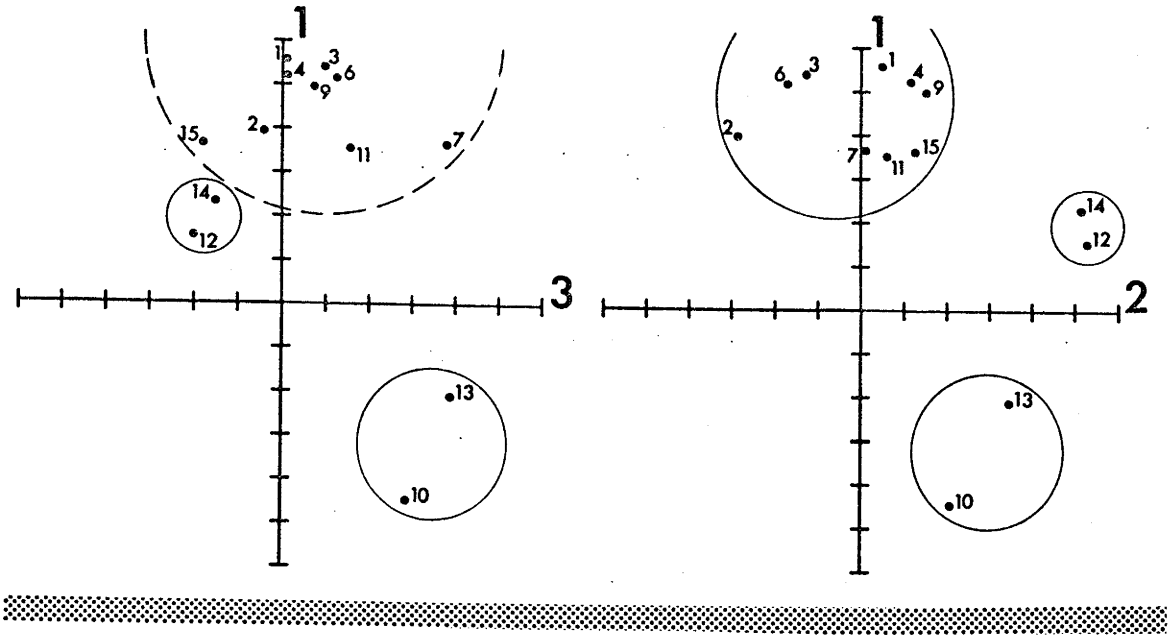

Figure 4.15: Scatter diagrams of the "response" wood character variables on the main principal components (z_{1-3}). The co-ordinates of each variable are the factor loadings on the respective components. Each axis is scaled to unit length, so the co-ordinates of each variable represent the magnitudes of the coefficients of correlation between the variable and the respective components.

The orthogonal linear combinations of variables show a general similarity to those derived from the same sample (but extended to include the variables' ring width and latewood ratio — see Table 4.3c, and compare Figures 4.3 and 4.15), which were interpreted in Section 4.2. The first 5 components account for 91% of the variance of the standardised data set; z_1 alone accounting for 49%.

The first 3 principal components, w_{1-3}, account for almost 100% of the variation of the standardised data set of the 5 "stimulus" variables (Table 4.18b). The 3 vectors represent height, radial position, and growth rate respectively.

The percentage of variance accounted for by each component will be influenced by the disproportionate weighting of some characters caused by the inclusion of closely similar measures, e.g., height in tree (absolute value) and percentage of tree height, and should not be taken to measure the relative variability of the characters that describe the respective components.

The first component, w_1, is essentially a vector representing height, and is almost completely correlated ($r = 0.99$) with each of the height measures.

w_2 is a vector of radial position very strongly associated with ring age (+0.93) and strongly (+0.73) with ring distance from the pith. The variation of growth rate contributes significantly to w_2, and the contrast between ring width (-.54) and the radial position variables is a result of collinearity in the systematic variation of these characters within trees (see Section 4.3).

The third principal component, w_3, is of particular interest because it is a vector representing growth rate that is independent of ring age ($r = .03$) and height (-.09, .01). The high positive affinity with w_3 of both ring width (+0.73) and ring distance from the pith (+0.53) are a result of the high degree of random differences between trees in radial growth rate. Thus, in trees that grow more rapidly (wide rings), the specific rings measured are more distant from the pith.

The coefficients of correlation, r_{zx}, of each of the first 5 response principal components (z_{1-5}) with the individual stimulus variables (x_{1-5}) are listed in Table 4.19.

Table 4.19: Coefficients of correlation, r_{zx}, between the first 5 principal components of the response characters (z_{1-5}) and the individual stimulus characters (x_{1-5}).

The multiple correlation coefficient, R, for response principal components × (combined stimulus characters) and the coefficient of determination, R^2, are listed.

	z_1	z_2	z_3	z_4	z_5
1 ring age	33	07	-28	36	27
2 pith distance	62	41	16	13	-26
3 % tree height	-47	-07	-26	05	07
4 height	-47	-01	-23	03	06
5 ring width	-49	32	38	-38	25
R	.76	.61	.56	.47	.37
R^2	.58	.37	.31	.22	.14

The correlation coefficients provide an index of affinity of each stimulus variable with each of the orthogonal linear combinations of response variables (see factor loadings of response variables in Table 4.18a). As was the case with the correlation analysis of individual stimulus and response variables, the coefficients provide a poor estimate of the relative importance of growth rate and radial position effects because of the collinearity of variation of these two characters within trees.

The multiple correlation coefficient, R, for each response principal component × (combined stimulus variables) is listed in Table 4.19. The moderately high values of R from the multiple regressions of each of the first 3 response components on the stimulus variables suggest that appropriate functions of the stimulus characters (height, radial position, and growth rate) would have some value in predicting meaningful combinations of response characters.

The first 3 eigenvectors, a, and partial regression vectors, b, which are required to complete the 3 equations (1) are shown in Table 4.20. The first of these equations, for example is:

$$.37\, y_{i1} + .26\, y_{i2} + .36\, y_{i3} + .35\, y_{i4} + .34\, y_{i6} + .24\, y_{i7}$$

$$+ .33\, y_{i9} - .30\, y_{i10} + .24\, y_{i11} + .10\, y_{i12} - .14\, y_{i13}$$

$$+ .16\, y_{i14} + .24\, y_{i15} = .48\, x_{i1} + .09\, x_{i2} - 1.0\, x_{i3}$$

$$+ .45\, x_{i4} - .19\, x_{i5} + \varepsilon_{i1} .$$

In contrast to the eigenvectors of the y-function, which have proved to be highly informative, an interpretation of the partial regression coefficients would seem inappropriate, especially in view of the close correlation between stimulus variables.

The coefficients of correlation between response variables or components and stimulus variables provided unreliable estimates of the relative importance of each stimulus variable because of the statistical interdependence (collinearity) of the response variables. This situation has proved an obstacle to the quantitative evaluation of the relative importance of radial position effects (ring age, distance from pith) and

Table 4.20: Eigenvectors, a, partial regression coefficients, b, and multiple correlation coefficients, R, for the equations of multiple regression of the first 3 response principal components (z_{1-3}) on the stimulus variables (x_{1-5}).

	a		
y_1	.37	.05	.01
y_2	.26	-.30	-.06
y_3	.36	-.13	.13
y_4	.35	.12	.02
y_6	.34	-.19	.18
y_7	.24	.01	.52
y_9	.33	.16	.10
y_{10}	-.30	.22	.39
y_{11}	.24	.07	.22
y_{12}	.10	.56	-.27
y_{13}	-.14	.37	.54
y_{14}	.16	.54	-.20
y_{15}	.24	.13	-.25

	b		
x_1	.48	-.51	-.23
x_2	.09	.84	.33
x_3	-1.0	-.36	.49
x_4	.45	.82	-.66
x_5	-.19	.13	.46
R	(0.76	0.61	0.56)

ring width, and has resulted in many examples in the literature of misinterpretation and confusion of the effect of age with the effect of growth [see reviews of Spurr, Hsiung, 1954; Elliott, 1970].

The principal components of the stimulus variables are, by contrast, statistically independent (orthogonal) and, as a consequence, indices of affinity (correlation coefficients) between the stimulus components and the response variables or components provide appropriate estimates of the relative importance of the relationship of each stimulus component with the response characters or character combinations. In the present example, the mutually orthogonal stimulus character combinations are readily interpreted to represent height, radial position, and growth rate (see previous discussion).

The product-moment correlation coefficients r_{zw}, for each z/w pair are presented in Table 4.21.

Table 4.21: Coefficients of correlation, r_{zw}, between the first 5 principal components of the response characters (z_{1-5}) and the first 3 principal components (w_{1-3}) of the stimulus characters.

	z_1	z_2	z_3	z_4	z_5
w_1	53	04	20	00	-10
w_2	54	11	-24	38	-33
w_3	02	56	46	-25	05

The multiple correlation coefficients, R, (Table 4.22) derived by substituting the principal components of the stimulus variables, w_ℓ, as independent variables in equation (1) are identical to those derived from the regressions of z_ℓ on the stimulus variables (Table 4.19). The partial regression coefficients are the coefficients of correlation of the dependent (z_ℓ) and independent (w_ℓ) variables and, since the independent variables are statistically orthogonal, the partial regression coefficients are readily interpreted. The eigenvalues, a_ℓ, required to complete the equations (1) are listed in Table 4.18a.

Table 4.22: Partial regression coefficients, multiple correlation coefficients, R, and coefficients of determination, R^2, for the equations of multiple regression of the first 5 response character principal components (z_{1-5}) on the stimulus components (w_{1-5}).

	z_1	z_2	z_3	z_4	z_5
w_1	.53	.04	.20	.00	-.10
w_2	.54	.11	-.24	.38	-.33
w_3	.02	.56	.46	-.25	.05
w_4	-.07	.20	.02	-.13	.01
w_5	.09	.06	.07	.04	-.13
R	.76	.61	.56	.47	.37
R^2	.58	.37	.31	.22	.14

The first response component, z_1, is strongly correlated with the first (0.53) and second (0.54) stimulus components, representing height and radial position respectively, but the correlation with w_3 (growth rate) is negligible (Table 4.21).

z_1 (Table 4.18a) is a linear combination of response characters that accounts for 49% of the variance of the standardised measures of all response characters. It is characterised by the strong correlation with the contrast of latewood tracheid wall thickness (0.83) and lumen diameter (-0.74) and the very high positive affinity of many of the densitometric characters (maximum density (0.93), mean density (0.90), density range (0.87), latewood percentage (0.83)). (N.B. A generally similar component, extracted from data set C (but including ring width and latewood ratio) is discussed in detail in Section 4.2.)

The variation of this linear combination of response characters (z_1) is interpreted as a response to position within the stem of individual trees. The moderately high correlation of ring width (*per se*) with z_1 (-0.49: See Table 4.19), and the moderately high loading of ring width on the first component (-0.57) extracted in the principal component analysis described in Section 4.2 (Table 4.4c), are primarily a result of co-response to a common factor, i.e., to position effects. The collinear variation of ring width with radial position is accounted for in the second stimulus component, w_2, but w_2 is much more strongly associated (0.93, 0.72) with radial position effects, particularly ring age (0.93) than with ring width (-0.54).

The combined stimulus components account for 58% of the variation of the linear combination of response characters on z_1 (Table 4.22).

The relationship of the second response component, z_2, with the combined stimulus components is also fairly strong (R = 0.61: Table 4.22).

z_2 accounts for 19% of the total variance of the response variables (Table 4.18a). It (z_2) is a vector closely associated with lumen width of earlywood tracheids (0.88) and, consequently, their overall C.S. size (0.86), but independent (in a statistical sense) of earlywood tracheid wall thickness (0.10) (Table 4.18a). There is a moderate negative affinity of z_2 with minimum (earlywood) density (-0.48),

indicating a complementary relationship where wide earlywood tracheids of variable wall thickness co-occur with wood of lowest density.

The correlation of z_2 with the stimulus components w_1 (0.04) and w_2 (0.11) is negligible, but the correlation of z_2 with w_3 (0.56) is of a high order (Table 4.21). This evidence is taken to indicate that the anatomical variation of the cells and associated low density of the earlywood described by z_2 is independent of within-tree position effects but is closely related to radial growth rate. It should be noted that w_3 is a vector which was extracted from the residual variation of the stimulus variables after removal of the variation associated with height and radial position effects, and is interpreted as a measure of radial growth rate *per se* (see previous discussion) which is strongly influenced by the random between-tree differences in growth rate.

31% of the variance of the third response component, z_3, is accounted for by the combined stimulus components (w_{1-5}) (Table 4.22).

z_3 accounts for 11% of the total variance of the response variables (Table 4.18a). It is a vector closely associated with the radial width of the latewood zone of the annual growth increment and with the overall C.S. dimensions of the latewood cells. Within the gradient of variation described by z_3, wider intra-incremental latewood zones are associated with wide latewood cells which tend to have relatively wide lumens but variable wall thickness.

z_3 is most closely correlated with the third stimulus component ($r = 0.46$: Table 4.21), but shows some correlation with w_1 (0.20) and w_2 (-0.24). This indicates that the variation of wood properties described by z_3 is most strongly influenced by growth rate (*per se*) but shows a relatively weak response to the effect of position within individual stems.

4.6 FEATURES OF THE GROWTH AND MORPHOLOGY OF THE TREES AND THEIR RELATIONSHIPS WITH SOME WOOD CHARACTERISTICS

The size of the trees at the time of sampling has been estimated from measures of tree height and average diameter over and under bark (measured by circumference tape) at breast height, 10%, 20%, 40%, 60%, and 80% of total tree height.

The volumes of stem sections between measurements were calculated as

$$\text{volume} = 0.5(s_1 + s_2) \times L ,$$

where s_1, s_2 are the sectional areas of successive measurement points and L is the length of section. The volume of the stem section between 80% of tree height and the stem apex was calculated as the volume of a right circular cone, and the basal diameter was determined by extrapolation to facilitate the estimate of the volume of the stem section below breast height.

Tree volume was calculated as the summation of the stem sectional volumes.

Parametric estimates of tree size are presented in Table 4.23.

Table 4.23: Parametric estimates of several size factors for the 20 trees of sub-plots A and B.

Stem character	Unit	Mean value	Range	s.d.	s.e.
Total height	ft.	64.6	49.0 - 72.0	5.94	1.33
d.b.h. (over bark)	inches	9.95	6.0 - 14.4	2.36	0.53
d.b.h. (under bark)	"	8.10	4.28 - 12.6	2.32	0.52
Basal area (o.b.)	sq.ft.	0.569		0.258	
" " (u.b.)	"	0.386		0.211	
Total volume (o.b.)	cu.ft.	16.82	4.67 - 33.39	8.17	1.83
Total volume (u.b.)	"	12.45	2.42 - 26.56	6.73	1.51
Bark volume	"	4.37	1.75 - 6.82	1.57	0.35
Merchantable volume (to 3" d.o.b.) (u.b.)	"	12.29	2.14 - 26.42	6.76	1.51

The 20 trees were selected from the overbark measures of diameter at breast height of 200 trees by ranked-set sampling (see (Chapter 2). The trees selected for study cover the range of d.b.h., and the properties of the selected sample resemble those of the parent population of sample measures (Table 4.24).

The features of the growth of the individual sample trees have been examined using the stem analysis techniques described in sub-section

Table 4.24: Parametric estimates of d.b.h. (o.b.) for the 20 sample trees and the population of 200 tree measures from which they were selected.

Parameters	Extracted sample	Total measured sample
n	20	200
Mean value (inches)	9.95	10.25
Range	6.0 - 14.4	6.0 - 14.7
s.d.	2.36	1.84
s.e.	0.53	0.13

4.3.13. The width of the annual growth rings were measured on the densitometric tracings. The stem radii used in the densitometric study were, in general, taken across a small diameter (see Chapter 3) and the samples were dried and extracted prior to measurement. As a result, estimates of stem diameter and volume increment in the stem analysis figures will underestimate the true values. The values should, however, provide reliable estimates for within- and between-tree comparison.

The patterns of growth of the individual trees are shown in Figures 4.16, 4.17, and 4.18.

It is readily apparent from the pattern of variation of the annual volume increment with age (Figure 4.16) and from the variation of total tree height with age (Figure 4.17) that the relative vigour (dominance status) of the trees is established at an early age (less than 10 years) and remains essentially similar with age. It should be noted that a gross increment, such as volume, reflects not only the amount of specific growth,* but also the size of the meristematic area.

The annual volume increment appears to have reached a maximum value and begun to decline progressively in the most strongly suppressed trees (i.e., trees A.9; B.9, 10).

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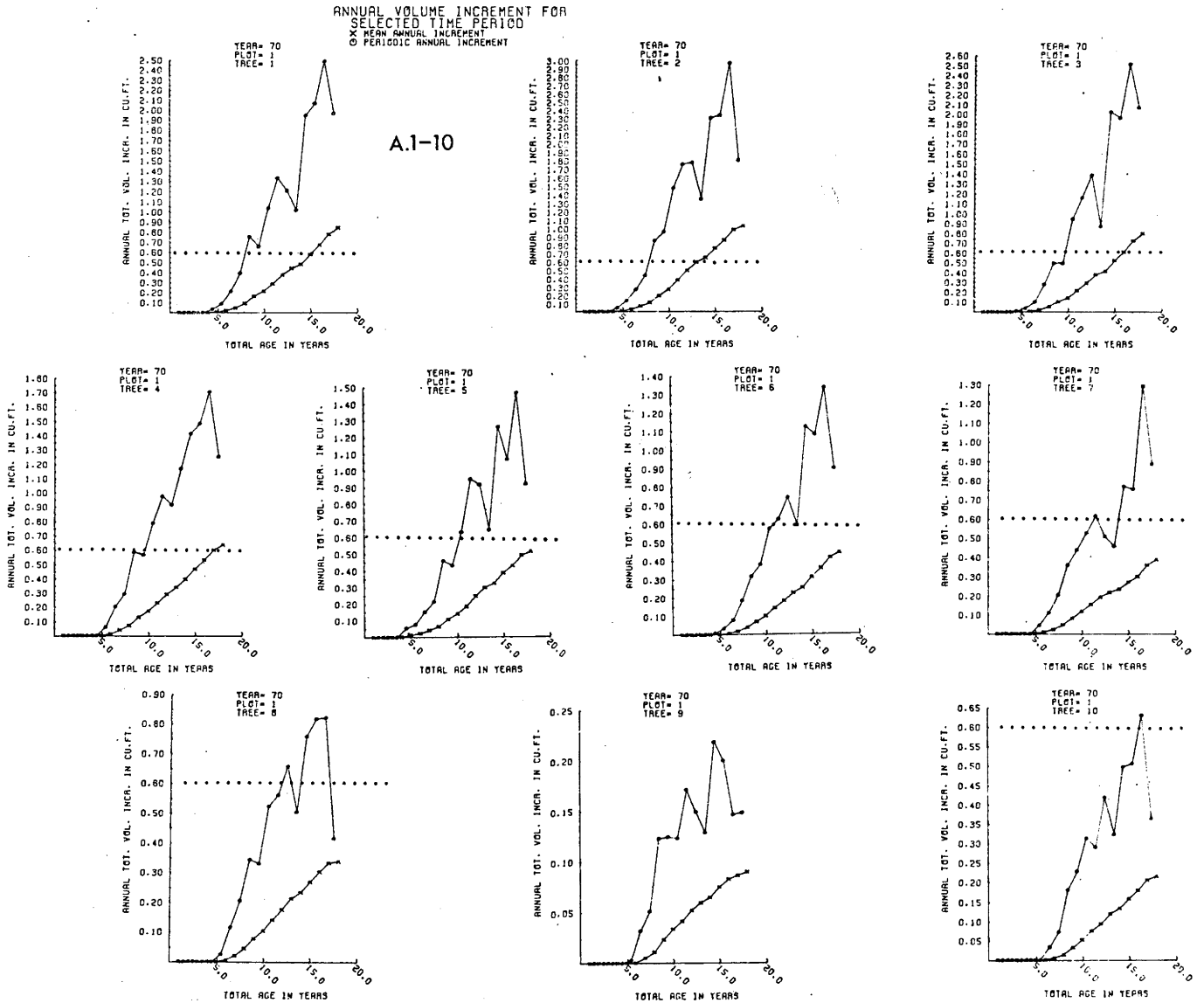
* Specific growth parameters are measures of "the rate of production per unit of that which is in active growth." [Duff, Nolan, 1957].


ANNUAL VOLUME INCREMENT FOR
SELECTED TIME PERIOD
X MEAN ANNUAL INCREMENT
O PERIODIC ANNUAL INCREMENT
A.1-10
YEAR= 70
PLOT= 1
TREE= 1
YEAR= 70
PLOT= 1
TREE= 2
YEAR= 70
PLOT= 1
TREE= 3
YEAR= 70
PLOT= 1
TREE= 4
YEAR= 70
PLOT= 1
TREE= 5
YEAR= 70
PLOT= 1
TREE= 6
YEAR= 70
PLOT= 1
TREE= 7
YEAR= 70
PLOT= 1
TREE= 8
YEAR= 70
PLOT= 1
TREE= 9
YEAR= 70
PLOT= 1
TREE= 10
ANNUAL TOT. VOL. INCR. IN CU.FT.
TOTAL AGE IN YEARS

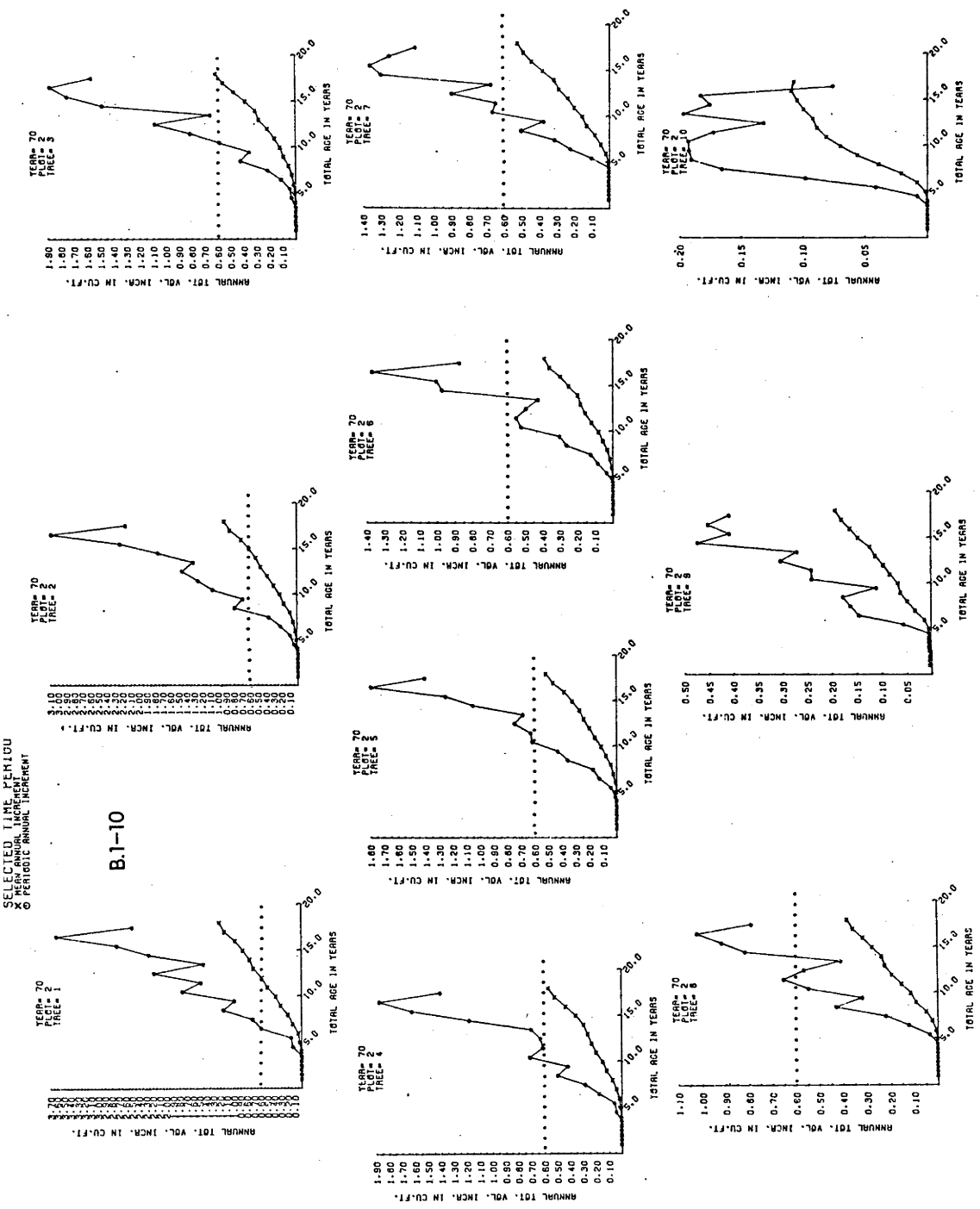
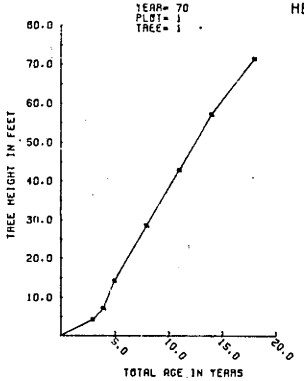
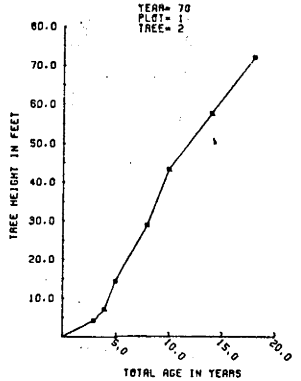


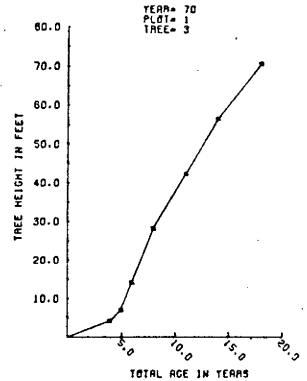
Figure 4.16: The annual volume increment (periodic and mean) of individual trees of plots A and B.

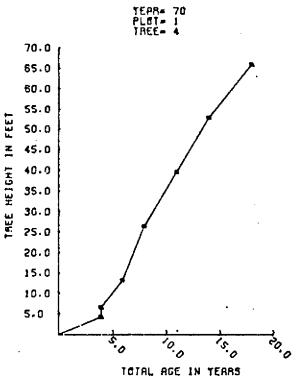
HEIGHT - AGE CURVE

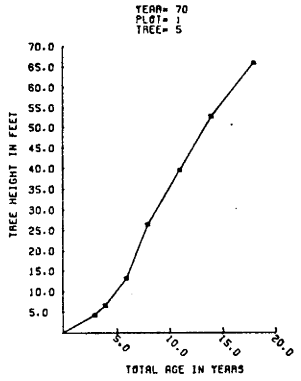
A.1-10

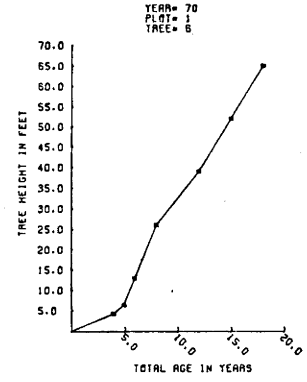


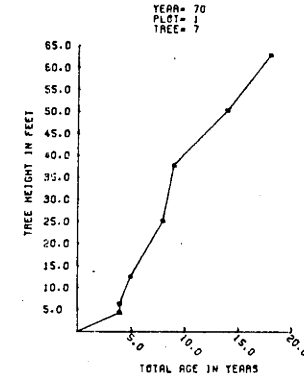


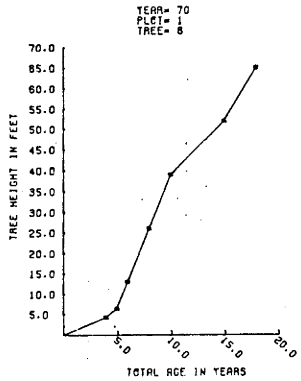


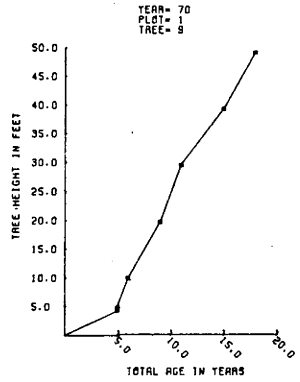


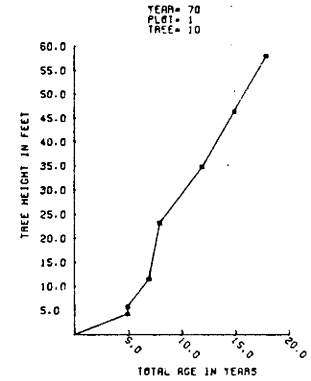












The outer growth rings are very narrow in the lower bole of the less vigorous trees (Figure 4.18). In tree B.10 the outermost annual growth increment was not detected below 40% of tree height.

The systematic pattern of decrease of ring width outward from the pith at a given height level, and from the upper to lower stem within an annual increment is apparent in Figure 4.18. The radial increment in the approximate region of the live crown over the age span fluctuates about a generally uniform value in most trees; the growth response of the trees showing little evidence of increase in eco-physiological stress as the stand ages.

The inter-correlation of the following growth and morphological features of the trees was examined:

x_1 — Tree height.

x_2 — Height to the base of the green crown (lowest complete green whorl).

x_3 — Length of the green crown ($x_1 - x_2$).

x_4 — Stem diameter at breast height (d.b.h.) under bark.

x_5 — Height/d.b.h. (x_1/x_4).

x_6 — Stem taper (the regression coefficient of the regression of stem C.S. area on height in the tree for percentile heights from 10% to 80%).

x_7 — Total stem volume under bark.

The variable x_6 is a reliable estimate of stem taper: There is a close linear relationship between C.S. area and height within the portion of stem above the butt swell [see Gray, 1944].

There is a high degree of correlation among the growth and morphological features (Table 4.25). Tree volume is very strongly correlated with height, d.b.h., and each of the two estimates of stem taper (viz., x_5, x_6). There is a strong degree of inter-correlation among these variables.

The wood density of the trees is most closely associated with stem taper (variables x_5 and x_6 in Table 4.26).

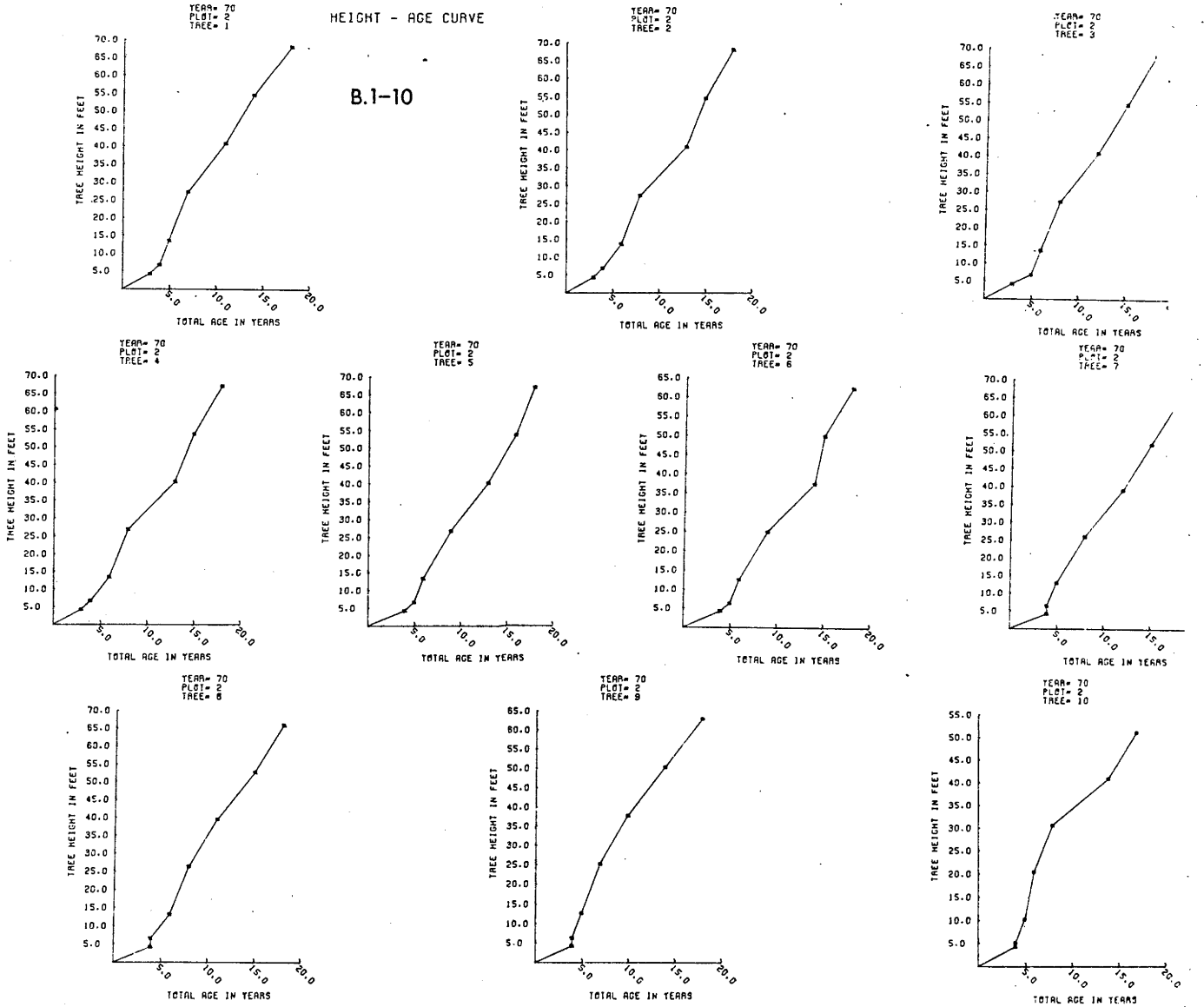
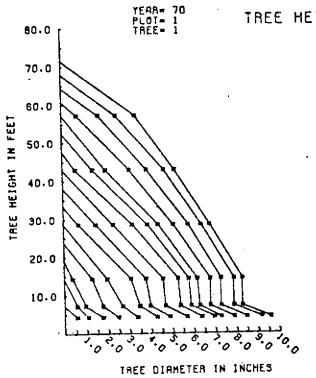
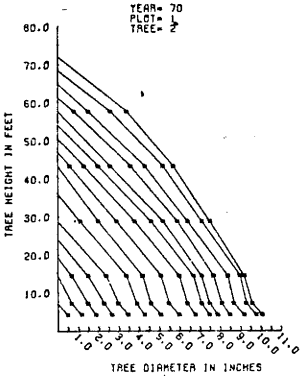


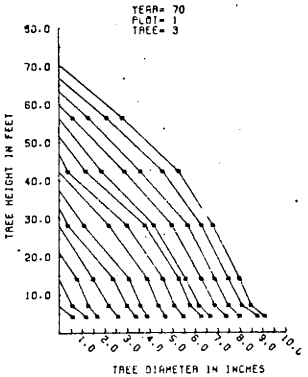
Figure 4.17: Height-age curves for individual trees of plots A and B.

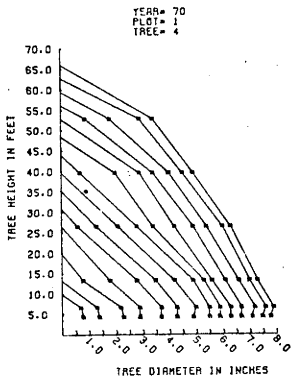
TREE HEIGHT VS. DIAMETER

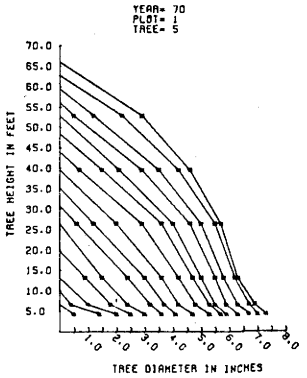
A.1-10

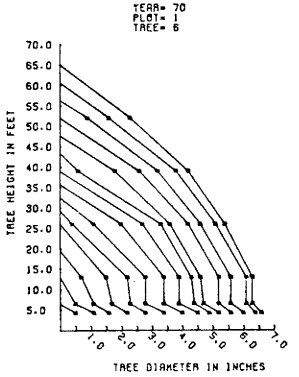


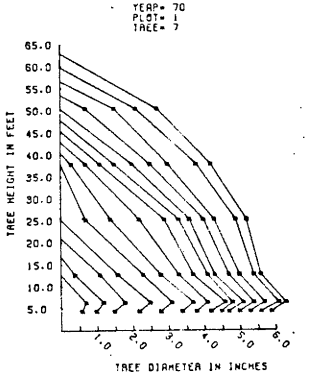


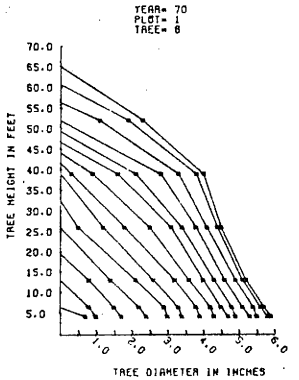


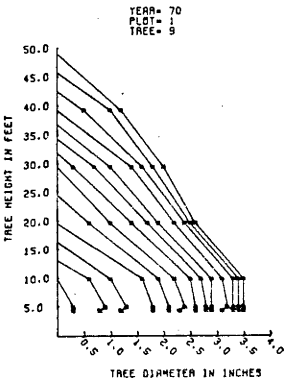


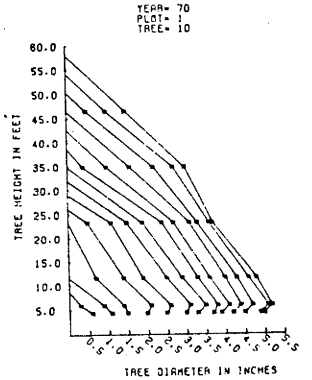












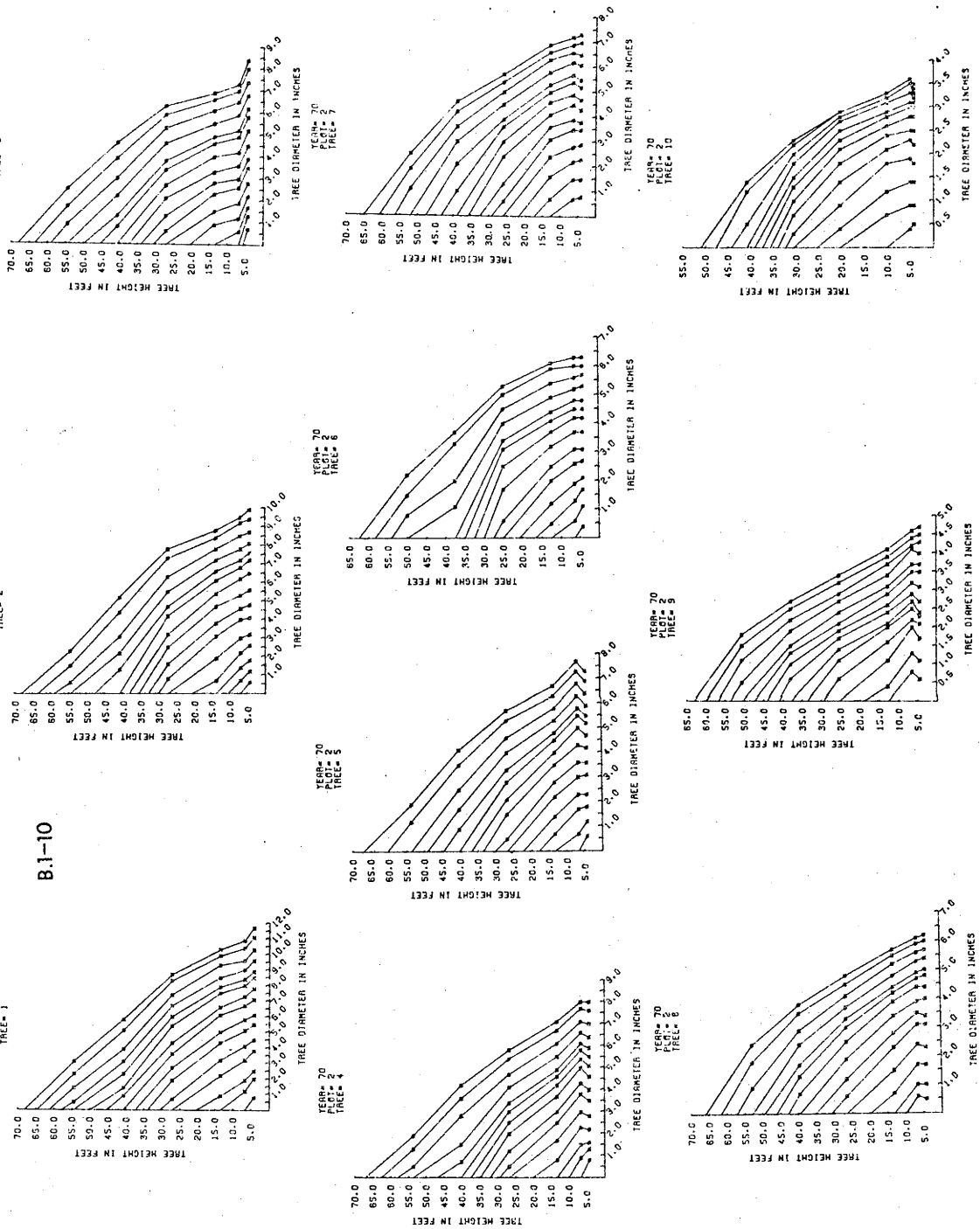


Figure 4.18: Tree height-diameter (taper) curves for individual trees of plots A and B.

Table 4.25: Correlations among morphological characteristics. The variable coding (x_{1-7}) is explained in the text.

	x_1	x_2	x_3	x_4	x_5	x_6	x_7
x_1		**	*	***	***	**	***
x_2	66			*	*		*
x_3	45	-37			*	*	
x_4	84	51	43		***	***	***
x_5	-82	-49	-44	-98		***	***
x_6	-62	-24	-48	-90	88		***
x_7	80	53	37	99	-96	-89	

Table 4.26: Coefficients of correlation between whole-tree wood density (weighted estimates) and several morphological characteristics.

	Variable	$r_{den.x}$
x_1	Tree height	-0.25
x_2	Crown base	-0.19
x_3	Crown length	-0.07
x_4	d.b.h.	-0.47 *
x_5	Height/d.b.h.	0.57 **
x_6	Stem taper	0.50 *
x_7	Stem volume	-0.45 *

A close relationship was observed in douglas fir (*Pseudotsuga menziesii*) between stem form and the variation of ring width, which was closely associated with earlywood development [Smith, Heger, Hejjas, 1966]. A similar relationship between stem form and wood density was observed by Larson [1963], who suggested that measures of tree or stem form might be of use in estimating the wood quality of trees. McKinnell [1970] noted a close association of stem taper with wood density in 14-year old trees of plantation-grown *Pinus radiata*.

There is a significant negative correlation between the wood mean density and the breast height diameter and total volume of the trees. Thus, the larger trees tend to have wood of lower density. Exceptions to this general tendency are apparent in a comparison of the growth estimates of individual trees (Figures 4.16 - 18) with their ranking on scales of wood density (e.g., in Figure 4.8). Trees A.1, 3; B.3, 5, for example, are vigorous dominants or codominants with wood of relatively high density. In contrast, trees A.4; B.1, 2 produce a large volume of wood of low density. The implications for tree breeding are important: There is considerable variation in the density features of the wood of trees that might be selected primarily for volume increment. There is also very considerable variation in the intra-incremental density contrast, an index of wood texture, among trees of comparably high vigour. In vigorous trees A.4; B.1, 2, 4 (Figure 4.16), for example, the wood is of very uniform texture (Figures 4.8 and 4.12), whereas in the comparably vigorous trees A.1, 2, 3; B.3 the intra-incremental density contrast is of a much higher order.

Whole-tree density is unrelated to tree height and the length of the living crown (Table 4.26). The size and distribution of the living crown are thought to be the principal intrinsic factors governing the patterns of growth and cell characteristics, and therefore wood density [Larson, 1962b, 1969]. But there are formidable difficulties in quantifying the relationships that exist between the living crown and gross estimates of the wood characteristics of trees (see discussion in sub-section 4.3.12.2).

4.7 SOME FEATURES OF THE NUTRIENT STATUS OF THE SOIL AND FOLIAGE, AND THEIR INTERRELATIONSHIPS WITH WOOD CHARACTERISTICS OF THE TREES

(a). Soil Nutrient Status : The Variation and Covariation Among Soil Nutrient Characters

Composite samples taken from the upper 10 cm of mineralised soil around the base of each of the 20 trees (see sampling schedule in Chapter 2) were analysed for nutrient status according to the techniques described in Appendix 2.

Parametric estimates of each topsoil character are presented in Table 4.27. The reference number of each soil character variable is retained throughout the presentation of the statistical analyses.

Table 4.27: Sample parameters of each of 11 topsoil characters. Nutrient values refer to the total levels of each element.

	Soil character	Unit	Mean value	s.d.	Maximum value	Minimum value	Coefficient of variation
1	Nitrogen (N)	ppm	266	101	572	129	37.9
2	Phosphorus (P)	ppm	3.0	5.4	17.0	0.0	180
3	Calcium (Ca)	ppm	235	195	1011	92.7	82.8
4	Potassium (K)	ppm	51.6	19.6	84.5	17.6	38.1
5	Magnesium (Mg)	ppm	60.9	39.0	126	8.1	64.0
6	Sodium (Na)	ppm	20.1	17.6	53.1	0.0	87.7
7	Iron (Fe)	ppm	1830	787	4364	971	43.0
8	Manganese (Mn)	ppm	15.9	4.1	26.4	9.4	25.8
9	Zinc (Zn)	ppm	2.6	2.1	8.7	0.0	80.2
10	pH		5.46	0.17	5.80	5.17	3.05
11	% Loss on ignition	%	1.81	0.61	4.06	1.22	33.8

There is a high degree of variation between samples for most elements.

The values of total phosphorus in the topsoil are very low. P was not detected in 13 of the 20 sample units (i.e., in 65% of sample locations). Na was undetected in 3 samples, and Zn undetected in 2 samples.

The low values of percentage loss on ignition indicate a low organic carbon content in the topsoil.

Coefficients of correlation, r_{xx}, between each soil character pair are presented in Table 4.28.

Table 4.28: Correlations among soil characters. The table is ordered to correspond with the principal component arrangement.

		11 % LI	7 Fe	1 N	5 Mg	4 K	2 P	3 Ca	6 Na	9 Zn	8 Mn	10 pH
11	% LI		***	***	*	*			*			
7	Fe	84		**	*		**					
1	N	78	59		*							*
5	Mg	44	46	50								
4	K	44	37	40	31							
2	P	43	56	24	14	-05		**				
3	Ca	22	27	24	39	-22	64					
6	Na	51	31	21	01	16	17	04				
9	Zn	17	08	26	40	14	-27	-00	-11			
8	Mn	05	21	08	34	03	-36	-03	-07	28		
10	pH	-16	-13	-52	-37	-20	12	11	06	-15	06	

The complex data of the matrix of inter-correlations among the soil characters have been resolved and reduced to relative simplicity (i.e., summarised) by principal component analysis.

The first 4 principal components of the soil characters are presented in Table 4.29.

Table 4.29: The first 4 principal components of the soil characters.

Principal component		w_1	w_2	w_3	w_4
Eigenvalue (λ)		3.74	2.07	1.43	1.17
Percentage of variance		34	19	13	10
Cumulative percentage		34	53	66	76
	Variable				
11	% LI	91	10	23	15
7	Fe	86	16	04	21
1	N	85	-17	08	-24
5	Mg	69	-31	-43	-07
4	K	49	-35	47	03
2	P	48	79	-16	-14
3	Ca	39	52	-65	-07
6	Na	38	27	51	39
9	Zn	26	-60	-32	08
8	Mn	14	-52	-38	60
10	pH	-35	44	-12	70

The affinity of each soil character variable with the main components is depicted graphically in Figure 4.19.

The first 4 components account for 76% of the total variance of the standardised soil character measures.

The first component, w_1, alone accounts for 34% of the total variation. w_1 is characterised by the very high positive affinity of % LI, Fe, and N: These variables are essentially independent of the variation of the remaining components. 5 of the 11 variables have their highest loadings on w_1. This group of soil characters (% LI, Fe, N, Mg, K) may be interpreted as a complex of soil characters which tend to co-occur in greatest and least abundance.

w_2 accounts for 19% of the total variance of the standardised soil character measures. w_2 is an orthogonal linear combination of soil variables that is characterised by the high loading on P (0.79) and the

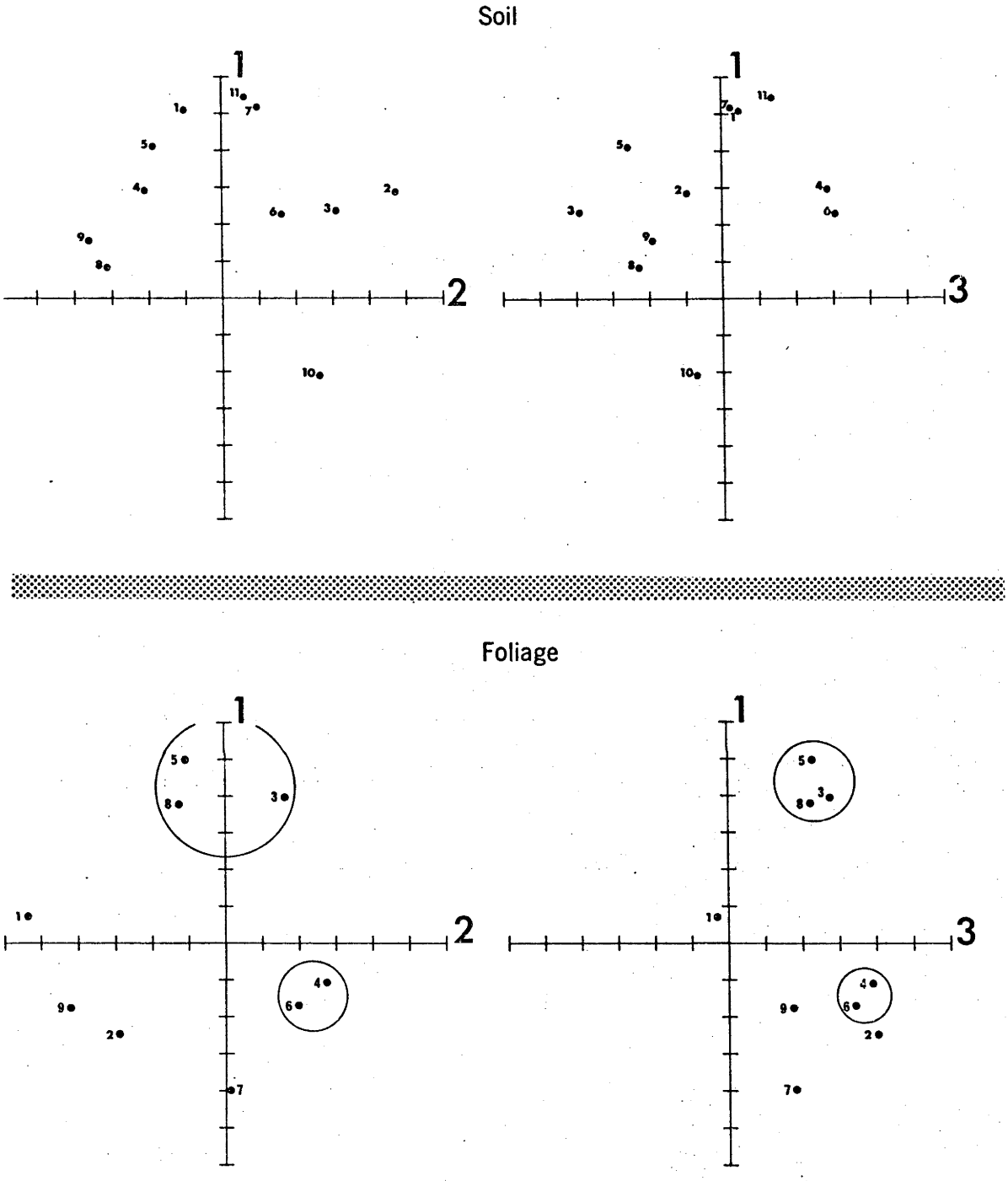


Figure 4.19: Scatter diagrams of (a) soil variables, and (b) foliage nutrient variables on their respective main principal components. The co-ordinates of each variable are the factor loadings on the respective components.

contrast between (P, Ca) and (Zn, Mn). It has a moderate positive affinity with pH.

w_3 and w_4 represent, respectively, 13% and 10% of the total variation of the standardised soil character measures, and are characterised by the contrast between Ca (-0.65) and Na (+0.51), and the positive association of pH and Mn, respectively.

The principal component analysis has effected useful resolution and an efficient summarisation of the simultaneous variation among the measured soil features. The effective dimensionality of variation has been reduced from 11 to 4 dimensions, each of which may be interpreted in terms of statistically independent linear combinations of the 11 original variables. These combinations are arranged in a form suitable for a study of their inter-relationships with the measures of foliar nutrient status and other plant attributes.

The technique of principal component analysis has been used to identify complexes of environmental factors in a number of studies [e.g., Austin, 1968; Cassie, Michael, 1968; Clunie, 1970; Barkham, Norris, 1970; Norris, 1971; Fourt, Donand, Jeffers, Binns, 1971].

Plant growth is a function of the inherent potential of the organism, and is an integrated response to the total (holocoenoic) environment. The variation of specific attributes of growth, such as wood characters or combinations of characters, will reflect the influence of complexes of interacting factors in the environment rather than single factors which have been arbitrarily dissected for measurement.

In the study of the response of growth attributes to the influence of the environment, the identification of environmental factor-complexes is informative, both in characterising the hypothesised "stimulus" complex in terms of the overall covariation among the measured factors, and in facilitating the estimate of relationships between the measures of growth response and complexes of stimulus factors, which may be more meaningful, in an ecological sense, than relationships between measures of growth response and individual stimulus variables.

(b) Foliage Nutrient Status: The Variation and Covariation Among Foliage Chemical Characters

Foliage samples (see sampling schedule in Chapter 2) from each of the 20 trees were analysed for nutrient status using the techniques described in Appendix 2.

Parametric estimates of each of 9 foliage nutrient characters are presented in Table 4.30. The reference number of each foliage nutrient is retained throughout the presentation of the statistical analyses.

Table 4.30: Sample parameters of each of 9 foliage chemical elements (measured as ppm).

	Foliage character	Mean value (ppm)	s.d.	Maximum value	Minimum value	Coefficient of variation
1	Nitrogen (N)	11033	1911	15438	8280	17.3
2	Phosphorus (P)	664	130	961	485	19.6
3	Calcium (Ca)	1646	563	3401	987	34.2
4	Potassium (K)	3216	2375	8462	723	73.9
5	Magnesium (Mg)	1364	344	2277	831	25.2
6	Sodium (Na)	1319	365	2124	638	27.7
7	Iron (Fe)	93.6	30.4	178.5	37.5	32.5
8	Manganese (Mn)	35.0	23.5	94.9	2.5	67.3
9	Zinc (Zn)	19.2	5.52	28.8	9.3	28.7

There is considerable variation between trees for most mineral elements. Potassium, in particular, is highly variable. The variation between samples is of a lower order than the variation of the corresponding elements in the soil samples for all elements other than K, the level of which is more variable in the foliage.

Foliage phosphorus levels are generally low (mean 0.066%; range 0.049% - 0.096%). "Critical levels" of phosphorus (defined as the foliar P concentration associated with 90% of maximum basal area increment) of 0.075 - 0.080% and 0.095 - 0.105% were set for *Pinus elliottii* and *P. taeda* respectively from a study of fertiliser trials

established using routine plantation techniques on Beerwah and Beerburrum State forests (i.e., within the immediate locality of the study plots) [Bevege, Richards, 1970].

The nutritional requirements of *P. caribaea* are not well understood, and there is little published evidence available for useful comparison with the results of the foliage nutrient estimates of the pines in this study. The published research of the nutrition of the species has been reviewed in detail by Lamb [1973; pp.111-117].

Coefficients of correlation, r_{yy}, between each foliage nutrient character pair are presented in Table 4.31.

Table 4.31: Correlations among foliar nutrient levels.
The table is ordered to correspond with the principal component arrangement.

		5 Mg	3 Ca	8 Mn	1 N	4 K	6 Na	9 Zn	2 P	7 Fe
5	Mg		**	**						
3	Ca	66								
8	Mn	56	36							
1	N	23	-16	16		*				
4	K	-05	22	05	-46					
6	Na	-04	14	-12	-26	30				
9	Zn	-02	-12	02	42	-09	-06		*	
2	P	03	-21	07	37	35	35	49		
7	Fe	-41	-13	-20	-15	19	22	29	32	
		Mg	Ca	Mn	N	K	Na	Zn	P	Fe

The extent of inter-correlation among the foliage nutrients is low. 4 of the 36 correlation coefficients are significant at the 5% level.

The information of the matrix of inter-correlations among the foliage characters has been resolved and reduced to relative simplicity by principal component analysis.

The first 3 principal components, v_{1-3}, of the foliage nutrients are presented in Table 4.32.

Table 4.32: The first 3 principal components of the foliage nutrient characters.

Principal component	v_1	v_2	v_3
Eigenvalue (λ)	2.33	1.99	1.87
Percentage of variance	26	22	21
Cumulative percentage	26	48	69
Variable			
5 Mg	83	-18	38
3 Ca	66	27	46
8 Mn	63	-21	37
1 N	12	-89	-05
4 K	-18	46	65
6 Na	-28	33	57
9 Zn	-29	-70	29
2 P	-41	-48	67
7 Fe	-66	02	30

The affinity of each foliage variable with the main components is depicted graphically in Figure 4.19.

The first 3 components account for 69% of the total variance of the standardised foliage nutrient character measures. Each of the foliage nutrient characters has its highest loading on one of the first 3 components: The remaining 6 components have been discarded because their loadings on the foliage variables are low, and the eigenvalue of each component is less than unity; i.e., less than the variance of each standardised variable.

The first component, v_1, accounts for 26% of the total variation. It is most closely correlated with the level of Mg ($r = 0.83$), and is characterised by the contrast between a group of positively associated characters (Mg, Ca, Mn) and 2 associated characters (Fe, P). Each of these groupings represent a complex of nutrients which tend to co-occur in greatest and least abundance. The positive and negative relationships of the respective groups with v_1 indicates a complementary feature in the relationship between the 2 complexes, i.e., where the elements of one complex tend to co-occur in greatest abundance, the elements of the other complex are simultaneously in lowest concentration.

v_2 accounts for 22% of the total variance of the standardised foliage chemical measures. v_2 is characterised by the strong affinity with N and Zn. Each of these characters is positively associated with P on v_2, and there is a contrast between this complex and K.

v_3 also accounts for a high portion of the total variation (21%). It is characterised by the strong positive affinity of P, K, and Na, each of which has its highest loading on v_3, and the moderate loading on Ca.

(c) Relationships Between the Levels of Nutrients in the Soil and Foliage

The principal component analysis of the foliage nutrient levels effects an ordination of the foliage characters on statistically orthogonal gradients of maximum variation among the measured characters. This arrangement facilitates the identification and estimate of the relationships between foliage and soil nutrient levels, using reasoning similar to that explained in Section 4.5.

The hypothesis is that the variation in the nutrient characteristics of the foliage is at least in part a response to the influence of the levels of the chemical elements in the soil. To the extent that the measures of the chemical elements are effective estimates of the nutrient levels of the soil and foliage, the relationships between them may be expressed in one or more meaningful linear equations (1).

Coefficients of correlation, r_{yx}, between each foliage and soil chemical character are presented in Table 4.33.

Table 4.33: Coefficients of correlation, r_{yx}, between foliar nutrient levels (p = 9 columns) and soil nutrients (q = 11 rows).

For n = 20 observations, the critical levels of r_{yx} are: 0.44 (0.05)*; 0.56 (0.01)**.

Multiple correlation coefficients, R, for foliar nutrient characters × (combined soil nutrients) are listed.

Soil		Foliage 1 N	2 P	3 Ca	4 K	5 Mg	6 Na	7 Fe	8 Mn	9 Zn
1	N	28	-04	-56	-34	-38	-34	08	-22	13
2	P	-30	20	-24	42	-20	06	17	-11	-14
3	Ca	-12	01	04	23	-09	-08	03	-04	02
4	K	41	-06	-40	-55	-14	-27	-15	-39	-02
5	Mg	16	02	-15	-35	-06	03	-28	-41	13
6	Na	-33	-13	-23	35	-07	-13	-22	15	-43
7	Fe	-13	-20	-38	-09	-26	-16	-06	-42	-05
8	Mn	-03	-32	01	-21	-09	-12	-26	-30	36
9	Zn	29	-15	03	-29	13	-29	-37	-18	24
10	pH	-32	-02	49	56	20	26	-04	-09	-26
11	% LI	-13	-18	-44	-04	-31	-28	01	-36	-23
	R	.78	.68	.76	.90	.53	.71	.73	.73	.74

The degree of inter-correlation is low. The correlation of 5 of the 99 foliage/soil character pairs is significant at the 5% level (11 of the coefficients exceed 0.4). The significant correlations involve only 2 of the 9 foliage elements, viz., Ca, which is negatively correlated with both soil N and % loss on ignition and positively correlated with soil pH, and foliar K, which is negatively correlated with soil total K and correlated positively with soil pH.

The multiple correlation coefficients, R, for foliage chemicals × (combined soil characters) range from 0.53 (foliar Mg) to 0.90 (foliar K), and are, in general, moderately high.

The coefficients of correlation, r_{vx}, of each of the first 3 foliage principal components (v_{1-3}) with the individual soil elements (x_{1-11}) are listed in Table 4.34.

Table 4.34: Coefficients of correlation, r_{vx}, between the first 3 principal components of the foliage nutrients (v_{1-3}) and the individual soil characters (x_{1-11}).

Multiple correlation coefficients, R, for foliage components × (combined soil characters) are listed.

		v_1	v_2	v_3
1	N	28	-28	-50
2	P	28	26	14
3	Ca	05	10	06
4	K	10	-30	-57
5	Mg	08	-15	-30
6	Na	-09	37	-06
7	Fe	21	12	-40
8	Mn	-02	-06	-30
9	Zn	-18	-29	-29
10	pH	-14	44	40
11	% LI	21	16	-43
	R	.58	.76	.79

The correlation coefficients are indices of affinity between the soil chemical characters and the complexes of foliage nutrient characters represented by the foliage components (Table 4.32).

The combination of foliage characters represented by the first component, v_1, is poorly predicted by the combined soil nutrient measures (R = 0.58), and the correlation of each of the soil variables with v_1 is low.

The moderately high values of the multiple correlation coefficient, R, for each of the second (0.76) and third (0.79) foliage components (v_2, v_3) × (combined soil nutrients) indicate a closer

relationship between the soil nutrients and the foliage nutrient complexes on v_2 and v_3, and suggest that appropriate functions of the soil nutrient variables would have some value in predicting these combinations of foliage characters.

v_2 is most closely correlated ($r = 0.44$) with soil pH.

v_3, which represents a positively associated complex of (P, K, Na, Ca) (see Table 4.32), has a postivie affinity ($r = 0.40$) with soil pH, and a negative affinity with each of the soil characters N (-0.50), K (-0.57), Fe (-0.40), and % LI (-0.43).

The correlation among the principal components of the foliage and soil characters is presented in Table 4.35.

Table 4.35: Coefficients of correlation, r_{vw}, between the first 3 principal components (v_{1-3}) of the foliage characters and the first 4 components (w_{1-4}) of the soil characters.

	v_1	v_2	v_3
w_1	24	-01	-44
w_2	08	46	43
w_3	-06	24	34
w_4	-14	33	-15

The first foliage (response) component, v_1, shows a negligible to low affinity with each of the soil (stimulus) components.

There is a moderately strong ($r = 0.46$) correlation of the second foliage component (v_2) with the second soil component (w_2). Zinc has a high loading (-0.70; -0.60) on the respective components.

The third foliage component, v_3, has a moderately high negative correlation (-0.44) with the first soil component (w_1) and positive correlation (+0.43) with w_2. v_3 and w_2 represent complexes of foliage and soil characters respectively which are most strongly characterised by the level of phosphate (see previous discussion).

The overall affinity of the nutrient levels of the soil and foliage is low. Only 2 of the foliage elements, calcium and potassium, are significantly correlated with nutrient factors in the soil. Both are positively correlated with soil pH. 81% and 57% of the variation of foliage K and Ca respectively are accounted for by the combined soil measures.

The inter-relationships between the foliage nutrient complexes and the soil factors and factor complexes are, in general, relatively weak, and difficult to interpret in terms of the effects of the measured soil features on the nutrient status of the foliage. In particular, the levels of specific elements in the foliage often bear little relation, or a negative relation (e.g., K) to the total level of these elements in the soil. Soil pH is related to the second and third foliage components which each represent, over 20% of the variation among the foliage elements.

The weakness of the relationships between the levels of nutrient elements in the soil and foliage, and the difficulty in interpreting the relationships that have been identified may, to a large extent, result from the inadequacy of measures of total levels of soil elements as indices of the availability of the nutrients for uptake by the plants. Measures of the cation exchange properties of the soil would, quite likely, have yielded more appropriate estimates of the effective nutrient status of the topsoil.

The restriction of soil samples to the uppermost 10 cm of mineralised soil may, to some extent, reduce the effectiveness of the soil measures as indices of nutrient availability. The top 10 cm of mineralised soil in general was found to represent the A (genetic) horizon with a slight protrusion into the uppermost B horizon. The topsoil was extensively permeated by fine rootlets. However, no information about the rooting systems of the trees is available. The development of a very small surface root system and abundant absorbing roots at deeper (perennial water table) levels was observed in *Pinus caribaea* var. *hondurensis* growing in plantations on deep porous sand in Zululand, South Africa [Haigh, 1966].

Pegg [1967] was unable to demonstrate a statistical relationship between slash pine (*P. elliottii*) site index and total P_2O_5 in the top 4 inches (10 cm) of soil over a wide range of sites which included areas in the Beerwah/Beerburrum Forests. He notes (i) a lack of significant correlation between soil measures of total and "available" P_2O_5, and (ii) that levels of foliar P from a phosphate trial on Toolara State forest (lat. 26° S) showed no relationship with total P_2O_5 values on a deep loamy sand lateritic podzolic soil.

(d) Wood Characteristics of the Trees: The Variation and Covariation of Wood Characters Between Trees

Large differences between trees in the phenotypic expression of each of the measured wood characters have been demonstrated. In this section the between-tree source of random variation of 12 wood characters is examined. An estimate is made of the relationships between the wood properties of the trees and the nutrient status of the foliage and soil.

The data set for the wood characters comprises the weighted whole-tree estimates of 6 densitometric characters (variables 1 - 7, Table 4.36) and the arithmetic whole-tree estimates of cell dimensions (variables 9 - 14). The calculation of these estimates is outlined in Section 4.4. Parametric estimates of the 12 characters are presented in Table 4.36.

There is a high degree of inter-correlation among the wood characters (Table 4.37).

The complex information of the matrix of inter-correlation is resolved and reduced to relative simplicity by principal component analysis. The first 4 principal components of the wood characters are presented in Table 4.38.

Each of the wood characters has its highest loading on either of the first 2 components, which together account for almost 80% of the variance of the standardised whole-tree estimates of all characters.

The first component, z_1, alone accounts for 52% of the total variation. z_1 is most highly correlated with mean density ($r = 0.96$) and latewood percentage (0.93). It is characterised by the close positive affinity of the densitometric characters and the strong correlation with

Table 4.36: The pooled mean estimates and standard deviations of the whole-tree values of 12 wood characters from the data of 20 trees. Parametric estimates of the densitometric characters (variables 1 - 7) were calculated from weighted whole-tree estimates; cell dimensions (9 - 14) from arithmetic whole-tree estimates.

	Wood character	Unit of measurement	Mean value	s.d.
1	Maximum density	g/cc	0.798	0.096
2	Minimum density	"	0.347	0.027
3	Mean density	"	0.495	0.044
4	Density range	"	0.450	0.087
6	Latewood percentage	%	36.82	11.67
7	Latewood width	mm	2.205	0.675
9	Latewood tracheid wall thickness	microns	15.73	1.820
10	Latewood tracheid lumen diameter	"	21.53	5.109
11	Earlywood tracheid wall thickness	"	8.610	0.850
12	Earlywood tracheid lumen diameter	"	49.48	4.76
13	Latewood tracheid width	"	37.29	4.099
14	Earlywood tracheid width	"	58.08	5.089

Table 4.37: Correlations among wood characters.

		3	6	1	2	9	4	7	11	14	12	13	10
3	DEN		***	***	***	***	**	*			*	**	***
6	% LW	96		**	***	**	*				*	***	***
1	DMAX	79	67		*	***	***	***					**
2	DMIN	88	94	46							*	**	**
9	LWW	71	59	87	41		***	*					***
4	DR	60	45	96	20	84		***					*
7	LWID	48	33	69	16	54	71						
11	EWW	33	35	35	33	36	29	34		*			
14	EWCD	-38	-43	-09	-42	03	02	11	46		***	**	*
12	EWL	-47	-52	-16	-51	-03	-03	05	32	99		***	*
13	LWCD	-62	-68	-40	-63	-40	-26	22	21	67	68		***
10	LWL	-75	-76	-64	-65	-68	-51	-02	04	52	55	94	
		DEN	% LW	DMAX	DMIN	LWW	DR	LWID	EWW	EWCD	EWL	LWCD	LWL

Table 4.38: Principal components of wood characters.

The components were extracted from the standardised whole-tree estimates of the 12 characters.

Principal component		z_1	z_2	z_3	z_4
Eigenvalue (λ)		6.27	3.11	1.21	0.90
Percentage of variance		52	26	10	7.5
Cumulative percentage		52	78	88	96
	Variable				
3	DEN	96	-07	18	11
6	% LW	93	07	33	08
1	DMAX	84	-45	-24	-00
2	DMIN	80	19	53	09
9	LWW	77	-46	-19	-26
4	DR	69	-55	-43	-03
7	LWID	43	-66	-24	54
11	EWW	23	-64	62	02
14	EWCD	-47	-78	20	-33
12	EWL	-54	-72	11	-35
13	LWCD	-74	-55	06	36
10	LWL	-87	-27	11	38

the contrast between the wall thickness (+0.77) and (lumen diameter (-0.87) and cell diameter (-0.74)) of the latewood tracheids.

There is one major source of variation in the data set from which the components were extracted; the random variation of the characters between trees. The characters with highest loadings of similar sign on a component represent a group of characters which tend to occur in highest and lowest value simultaneously, i.e., in the same trees.

High loadings of opposite sign on a component indicate a complementary feature in the relationship: The characters (or variables of the character group) of one sign tend to increase in value as characters of the opposite sign decrease. Thus the values of the wood characters (mean, maximum, and minimum density, latewood percentage, density range, and latewood tracheid wall thickness) tend to be

simultaneously high in trees in which the lumen width and overall diameter of latewood tracheids is low (and *vice versa*).

The second component, z_2, accounts for 26% of the total variation. z_2 is an orthogonal linear combination of variables most strongly representing variation in the C.S. dimensions of the earlywood tracheids. There is a close positive association of wall thickness, lumen diameter and overall diameter. Thus, in a given tree, the wider the earlywood tracheids the thicker their walls tend to be. Latewood width has its highest loading on z_2.

z_3 accounts for 10% of the total variation. It is most strongly correlated with earlywood tracheid wall thickness (0.62) and minimum (earlywood) density (0.53).

(e) Relationships Between the Wood Characteristics and Foliage Chemical Levels of the Trees

The extent of inter-correlation between the wood characters and foliage chemicals is rather low (Table 4.39). 10 of the 108 coefficients of correlation exceed 0.4, and 7 are significant at the 5% level.

Table 4.39: Coefficients of correlation, r_{yx}, between 12 wood characters (whole-tree values) and 9 foliar chemicals.

For n = 20 observations, the critical levels of r_{yx} are: 0.44 (.05)*; 0.56 (.01)**.

Multiple correlation coefficients, R, for wood characters × (combined foliar chemicals) are listed.

		1 DMAX	2 DMIN	3 DEN	4 DR	6 % LW	7 LWID	9 LWW	10 LWL	11 EWW	12 EWL	13 LWCD	14 EWCD
1	N	-13	-07	-11	-13	-07	-02	-20	08	-23	-33	01	-34
2	P	-10	-11	-10	-08	-17	17	-35	30	-17	-14	22	-16
3	Ca	-19	02	-15	-21	-09	04	-00	29	41	48	36	51
4	K	-27	-18	-27	-24	-28	-13	-26	40	24	52	37	52
5	Mg	-17	03	-13	-20	-12	-15	-07	11	-04	17	10	15
6	Na	22	23	21	17	14	33	07	14	26	21	21	24
7	Fe	10	-37	-20	22	-26	52	-18	49	10	21	53	21
8	Mn	-04	32	20	-15	16	-00	08	01	12	03	04	04
9	Zn	01	-41	-20	13	-33	28	-01	19	-19	-08	23	-11
R		.54	.83	.74	.54	.73	.69	.61	.77	.64	.82	.80	.83

The significant correlations involve 3 foliage elements:

The level of foliage calcium is positively correlated with the lumen diameter ($r = 0.48$) and cell diameter (0.51) of the earlywood tracheids. There is a moderate positive correlation of foliage Ca with earlywood tracheid wall thickness (0.40) and latewood tracheid diameter (0.36).

Foliage potassium is also positively correlated with the lumen diameter (0.52) and cell diameter (0.52) of the earlywood tracheids, and shows a moderate positive correlation with the lumen diameter (0.40) and cell diameter (0.37) of the latewood tracheids.

The level of iron in the foliage is positively correlated with the width of the intra-incremental latewood zone (0.52) and with the lumen diameter (0.49) and cell diameter (0.53) of the latewood tracheids (cf., the low negative correlation of Fe with latewood tracheid wall thickness). There is a moderate negative correlation (-0.37) of Fe with minimum (earlywood) density.

The correlations of the remaining foliage elements with the wood characters are generally low. Foliage Zn has a moderate negative affinity with minimum (earlywood) density.

The multiple correlation coefficients, R, for wood characters × (combined foliage elements) exceed 0.7 (Table 4.39) for 7 of the 12 wood characters, indicating that over 50% ($R^2 \times 100$) of the variation in these characters can be predicted (is accounted for) by the combined measures of the foliage elements. The coefficient of determination, R^2, is highest for the lumen and cell diameters of both earlywood (.67, .69) and latewood (.59, .64) tracheids and minimum (earlywood) density (.69); i.e., roughly 60% to 70% of the variation between trees in these wood characters is predicted by the combined foliage nutrient measures.

The correlation of the main principal components of the wood characters (z_{1-3}) with individual foliage elements is, in general, low (Table 4.40).

z_1 is not strongly correlated with any of the foliage elements. The multiple correlation coefficient, R, for z_1 × (combined foliage elements) is relatively low (0.69; $R^2 = .48$). This suggests that the

Table 4.40: Coefficients of correlation, r_{zx}, between the first 3 principal components of the wood characters (z_{1-3}) and 9 foliar chemical characters (x_{1-9}).

Multiple correlation coefficients, R, for wood components × (combined foliar characters) are listed.

	z_1	z_2	z_3
1 N	-06	27	-16
2 P	-16	08	-13
3 Ca	-23	-35	45
4 K	-38	-26	33
5 Mg	-15	01	14
6 Na	09	-34	20
7 Fe	-23	-41	-26
8 Mn	08	-01	34
9 Zn	-14	-08	-49
R	.69	.72	.83

major gradient of variation among the wood characters is not closely related to the levels of the measured elements in the foliage.

z_2 shows a moderate negative affinity (-0.41) with Fe, Ca, and Na, but the correlation of z_2 with the other elements is generally low. The combined elements account for 52% ($R^2 \times 100$) of the variation of z_2.

The correlation of z_3 with Ca (0.45) and Zn (-0.49) is of a moderately high order. 69% of the variance of z_3 is accounted for by the combined foliage elements. z_3 represents variation of earlywood tracheid wall thickness and minimum (earlywood) density.

The correlation between the principal components of the wood characters and those of the foliage elements is presented in Table 4.41.

The first wood character (response) component, z_1, has negligible to low affinity with each of the foliage (stimulus) components.

There is a moderate negative correlation (-0.34) of z_2 with the third foliage component (v_3). This may be interpreted as a positive (N.B., the negative loadings of EWW, EWL, EWCD on z_2) association of the C.S. dimensions of the earlywood tracheids with a foliage nutrient complex of (P, K, Na, Ca).

Table 4.41: Coefficients of correlation, r_{zv}, between principal components of wood characters (z_{1-3}) and components of foliage characters (v_{1-3}).

	z_1	z_2	z_3
v_1	03	09	37
v_2	02	-28	39
v_3	-29	-34	22

The third wood character component, z_3, shows a moderate positive affinity with the first (0.37) and second (0.39) foliage components (v_1, v_2). These relationships are of limited interpretive value as z_3 accounts for a relatively small portion of the between-tree variation in the wood characters. z_3 represents variation of earlywood tracheid wall thickness and minimum (earlywood) density.

In Summary

There is a moderately strong relationship between the foliage nutrient levels and the lumen and cell diameters of the tracheids; the strongest relationships involving these anatomical characteristics of the earlywood cells. The relationships appear to effectively involve few of the foliage elements examined. Thus, earlywood tracheid lumen and cell diameters show a close positive association with foliar calcium and potassium levels. Ca is positively associated with earlywood tracheid wall thickness also.

The level of iron in the foliage is strongly associated with the latewood tracheid lumen and cell diameters. Foliage K shows a moderate positive association with these anatomical traits. The relationships of the foliar elements with wall thickness of the latewood tracheids are, in contrast, weak or negligible.

Of the densitometric characters, minimum density shows some relation to the overall nutrient status of the foliage, and the width of the intra-incremental latewood zone is positively associated with the level of foliar Fe, but the relationships of the other characters with the foliage nutrients are poorly defined.

The first principal component of the wood characters, a linear combination of the variables on the major gradient of variation in the variable set, has a weak to negligible affinity with each of the foliage elements and combinations of elements. The first wood component is closely related to the variation of the densitometric characters, most of which have a weak, poorly defined relationship with the foliage elements.

The second and third components of the wood characters, which are most closely related to the anatomical characteristics of the earlywood tracheids, show some affinity with foliage elements (z_2 with Fe, Ca, Na; z_3 with Ca, Zn, K, Mn) and with complexes of foliage elements. But the relationships, although consistent, are relatively weak.

(f) Relationships Between the Wood Characteristics of the Trees and Nutrient Factors in the Soil

The trees and their immediate habitat form an integrated complex existing at a specified location in space. For analytical purposes, it is expedient to distinguish three elements of the system; viz., the plants, the sites in which the plants occur, and the environmental features associated with these sites [see Lambert, Dale, 1964]. The elements of the plant/site/habitat (i.e., vegetation) system may each be analysed separately, and their inter-relationships then determined.

This system of analysis is used here to assess the inter-relationships of wood characteristics and soil factors. A generally similar systems approach is, indeed, implicit in each of the analyses of this study that involve "stimulus" and "response" characteristics.

Since the soil sample units were extracted from around the base of each sample tree, the sites may effectively be regarded as common to both: This facilitates a statistical analysis of the inter-relationships of the plant (wood characters) and habitat (soil features) elements.

The statistical analyses of the inter-relationships accord with reasoning similar to that discussed in Section 4.5.

The degree of correlation between the wood characters and the soil nutrient factors is low (Table 4.42). 3 of the 132 correlations

exceed 0.4, and only one of these, the positive correlation of earlywood tracheid wall thickness with soil pH (r = 0.49), is significant at the 5% level.

Table 4.42: Coefficients of correlation, r_{yx}, between 12 wood characters (whole-tree values) and 11 soil nutrient factors.

For n = 20 observations, the critical levels of r_{yx} are: 0.44 (.05)*; 0.56 (.01)**.

Multiple correlation coefficients, R, and coefficients of determination, R^2, for wood characters × (combined soil factors) are listed.

		1 DMAX	2 DMIN	3 DEN	4 DR	6 % LW	7 LWID	9 LWW	10 LWL	11 EWW	12 EWL	13 LWCD	14 EWCD
1	P	-05	-21	-06	01	-14	-14	-17	-05	-42	-28	-13	-33
2	N	15	-06	07	19	03	-00	08	-14	-18	-01	-15	-04
3	Ca	05	03	08	05	05	-04	08	-07	02	-15	-05	-14
4	K	21	-04	08	25	09	06	14	-27	-16	-34	-28	-34
5	Mg	-00	-11	-01	03	-07	-20	01	-17	-25	-36	-21	-38
6	Na	09	10	11	07	02	-24	07	-17	-03	02	-18	02
7	Fe	07	-23	-08	15	-12	-24	03	-20	-27	-12	-24	-16
8	Mn	12	-09	01	15	-02	-10	25	-24	15	-03	-18	-01
9	Zn	-32	-24	-32	-28	-30	-39	-24	05	-09	-14	-04	-15
10	pH	09	14	05	05	14	08	07	02	49	36	06	42
11	% LI	-03	-22	-12	04	-15	-30	-17	-09	-25	-14	-19	-17
	R	.57	.42	.49	.58	.43	.61	.66	.57	.63	.55	.48	.57
	R^2	32	18	24	34	18	37	44	32	40	30	23	32

The combined soil nutrient measures account for a small portion of the variance (18% to 44%) of each of the wood characters; i.e., the relationships between each of the wood characters and the soil nutrients are weak or almost negligible.

The relationships between the wood components and the soil factors are, in general, weak or negligible (Table 4.43).

Table 4.43: Coefficients of correlation, r_{zx}, between the first 3 principal components of whole-tree wood characters (z_{1-3}) and 11 soil nutrient factors (x_{1-11}).

The coefficient of determination, R^2, for wood components × (combined soil factors) are listed.

	z_1	z_2	z_3
1 N	-04	30	-38
2 P	09	02	-24
3 Ca	09	06	-03
4 K	22	16	-35
5 Mg	06	31	-29
6 Na	08	06	02
7 Fe	02	18	-38
8 Mn	11	-04	-10
9 Zn	-23	29	-04
10 pH	02	-34	40
11 % LI	-06	24	-26
R^2	.27	.22	.44

The combined soil factors account for only 27% and 22% of the variation of the first (z_1) and second (z_2) wood components. The correlation of each of the soil factors with z_1 is very low (Table 4.43). Soil pH has a moderate negative affinity ($r = -0.34$) with z_2. This indicates a relatively weak positive association of soil pH with the anatomical characteristics of the earlywood tracheids (each of which has a strong negative affinity with z_2: Table 4.32).

The third component, z_3, has a closer affinity with the soil factors: 44% of the variations of z_3 is accounted for by the combined soil features. Soil pH is positively associated with z_3, which largely represents variation in earlywood tracheid wall thickness and minimum (earlywood) density. There is a moderate negative correlation of soil N (-0.38), K (-0.35), and Fe (-0.38) with z_3.

There is a weak to negligible relationship between each of the soil components (w_{1-4}) and the first wood component, z_1 (Table 4.44).

Table 4.44: Coefficients of correlation, r_{zw}, between the first 3 principal components of wood characters (z_{1-3}) and the first 4 components (w_{1-4}) of soil nutrient factors.

Multiple correlation coefficients, R, for wood components × (combined soil components) are listed.

	z_1	z_2	z_3
w_1	.04	.31	-.41
w_2	.07	-.19	.12
w_3	-.05	.02	.05
w_4	.07	-.20	.21
R	.52	.47	.66

The first soil component, w_1, shows some affinity with each of the second (r = 0.31) and third (-0.41) wood components. w_1 represents a complex of (% LI, Fe, N, Mg, K ... Table 4.29) which is negatively related to the third foliage component. The relationships are relatively weak and difficult to interpret.

In Summary

The relationships between the measured soil features and the wood characteristics of the trees are generally negligible or weak and poorly defined. There is some relationship between the anatomical characteristics of the earlywood tracheids and the measured soil features; a relationship most consistently associated with soil pH, which has a moderately strong positive affinity with the wall and lumen dimensions of the earlywood tracheids.

In contrast to the consistent relationships between the foliage levels of specific nutrient elements (Ca, K, Fe) or combinations of elements and the anatomical characteristics of the earlywood and latewood tracheids, the levels of specific elements in the soil bear little or no relationship to the measured wood features. The low extent and degree of association of the wood characteristics of the trees with the soil elements may, to a large extent, reflect the analytical technique: The measures of soil total element levels may not provide appropriate estimates of the availability of nutrients for uptake by the trees, even over a long period. The degree to which the topsoil effectively

represents the volume of soil penetrated by the bulk of absorbing rootlets, and the relative levels of nutrients available for uptake within this undefined vertical sequence are unknown variables which may lessen the effectiveness of the soil samples as estimates of the nutrient status of the soil in relation to the growth response of the plants; these factors would vary greatly between soil types, and could be of particular significance in a highly porous, sandy soil. These possible shortcomings of sampling and analytical technique were discussed in relation to the low degree of affinity between specific elements in the soil and foliage (subsection 4.7c).

Technical difficulties associated with soil analysis are avoided in the analysis of foliage material: The nutrient levels of the foliage may be considered to be an integrated result of soil nutrient availability and physiological uptake. The extent to which the internal nutrient requirements of trees alter with age, if at all, is unknown [Tamm, 1964]. The same "critical levels" (see above) of foliar P were found to apply to stands of *Pinus elliottii* and *P. taeda* ranging in age from under 10 years to over 30 years in the Beerwah/Beerburrum plantations [Bevege, Richards, 1970].

It is of interest to note that the soil factor showing a consistent relationship with the earlywood tracheid dimensions, i.e., soil pH, has a strong positive affinity with each of the foliage elements (Ca, K) that were shown to be closely related to these characteristics of the wood anatomy.

CHAPTER 5

GENERAL DISCUSSION

Very little information about the structural features of the wood of var. *hondurensis* was available when this research programme began. In recent years a great deal of research effort has been directed towards acquiring an understanding of the variation of features of the wood that will affect its processing and utilisation.

Some indication of the range and extent of variation in some important characteristics of the wood of trees from the native forests of British Honduras is now available [Hughes, 1970], and a detailed assessment has been made of the variation of several important anatomical and structural attributes of the wood within and between 30-year old trees from a natural stand [Lantican, 1971]. Important inferences about the nature of variation of wood characteristics of var. *hondurensis* can be drawn from the results of these studies. The overall variation of structural features is of a high order. Pronounced phenotypic variation in the average values of specific wood characters and in their pattern of development are evident between trees growing on the same sites; a feature of variation that suggests a considerable degree of heritable differences between trees. Marked differences in cyclic growth behaviour, latewood development, and tracheid length between populations growing on different sites are suggestive of a tendency for these features to vary in response to different environmental conditions.

These aspects of variation, viz., the genetic and environmental components, and their interaction, are accentuated in the introduction of the species to a wide range of new habitats in programmes of exotic afforestation in the tropics and subtropics. The response of growth and of form is manifest as a wide range of variability [see compiled reports of Burley, Nikles, 1973 a,b; Lamb, 1973]: This includes aberrant growth forms, for example "foxtailing"; a form of apical dominance that results from the failure to set buds that would elongate to form lateral shoots [Kozlowski, Greathouse, 1970].

The genetic aspect of variation offers potential for tree improvement through selection and breeding, and this has been realised to some extent in Queensland, in improved stem straightness, crown form, and vigour [Slee, Nikles, 1968; Nikles, 1973b]. A high degree of inherent variability in var. *hondurensis* in its natural range [see, e.g., Luckhoff, 1964; Nikles, 1966; Kemp, 1970] is reflected in the variable growth response of provenances established as exotics in trial plantings [see Nikles, 1973a]. But little is yet known of the environmental tolerances and relative growth of selected populations: There is evident potential for increasing volume yield and for improving morphological characteristics by the matching of selected populations with suitable site conditions, and a comprehensive international programme of provenance trials has been instituted recently [Kemp, 1970].

The known growth characteristics of the species provide a sound indication of its potential for rapid cellulose production in an extensive range of environments.

The wood of var. *hondurensis* is known to vary quite markedly in structure and properties within the wide range of habitats encountered in exotic plantings in the tropics and subtropics. Large differences in specific wood characteristics between trees from the same plantings and between stands established on sites of diverse nature have been demonstrated. The degree of variability of wood characteristics encountered in var. *hondurensis* is unusually great among commercially important coniferous species: This variability is a potential source of problems in processing and utilisation; but it offers interesting possibilities for increased control of wood quality by selection of suitable genotypes and by the effective matching of selected populations with favourable site conditions.

What tests are available have in general implicated the suitability of the wood of young trees from exotic plantings for the production of reconstituted fibre products. Much less is known of the structure and related properties of older material that will affect its suitability for sawlog and plylog production: The limited experience of timber properties is confined to material over about 18 years of age*

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* There are very few exotic plantings of *Pinus caribaea* older than this.

from subtropical regions of South Africa [e.g., Scott, 1952;* Luckhoff, 1964; de Villiers, 1973] and southern Queensland [Smith, 1973].

The variation of important structural features of the wood of plantation-grown var. *hondurensis* is known to be of a high order; but there n few detailed studies made of the nature of this variation. The patterns of variation of wood mean density and tracheid length were examined in 10-year old trees from plantations established on two soil types in Jamaica [Brown, 1969, 1973; Burley *et al.*, 1973]: To the author's knowledge these studies, and the research reported in this thesis, comprise the only detailed information available of the patterns of variation of these features within trees from exotic plantations. The variation of wood density and tracheid length between trees has been estimated in a number of other studies, but the estimates have in general been derived from measures of small samples taken from a single level in the lower stem of individual trees, and the extent to which these samples are representative of whole-tree values in unknown.

The study by Lantican [1971] of ten 30-year old trees from a natural stand in British Honduras is the only other detailed examination of the patterns of variation of tracheid cross-sectional dimensions in var. *hondurensis* with which the author is familiar. There is little comparative evidence available of the nature of variation of tracheid cross-sectional dimensions in coniferous species: The present work provides a significant contribution towards the development of an area of research, the importance of which is widely recognised, but in which present knowledge is obviously wanting.

The technique of X-ray densitometry has proven versatile in extending the study of wood density patterns to include precise measures of the intra-incremental density range and extreme values. These features are valuable aids to resolving the nature of wood density variation, and are themselves important indices of wood texture; a characteristic related to properties that include veneer peeling quality, machineability, pulp quality, and mechanical and weathering properties of the wood.

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* N.B. The taxonomy of the species of trees described by Scott has since been revised: His *Pinus caribaea* refers to *P. elliottii*, and *P. hondurensis* refers to *P. caribaea* var. *hondurensis*.

A comprehensive range of densitometric features (maximum, minimum, and mean density; density range; latewood percentage; width of the latewood zone; ring width; latewood ratio) and anatomical characteristics (tracheid radial double-wall thickness, lumen and cell widths in the earlywood and latewood; earlywood tracheid length) of the annual growth increments from selected positions within twenty 18-year old trees was examined.

The inter-relationships among the complex of wood characters were identified and estimated using simple correlation analysis and a multivariate model, namely principal component analysis. The results of the analyses, and the inference and conclusions derived from them, are discussed in Section 4.2. The principal component technique effected an efficient summary of the variation and covariation in the character complex: The effective dimensionality of variation was reduced from 15 to 3 dimensions, each of which was interpreted in terms of statistically independent linear combinations of the original 15 variables. The identification and estimation of inter-relationships among the wood characters proved useful in the generation of hypotheses about possible causal mechanisms underlying these relationships.

The patterns of variation of individual wood characters within each of the twenty trees were examined. The results are presented and discussed in Section 4.3. Many of the characters exhibit pronounced systematic variation within individual stems. Much of this variation is associated with the age of the cambium at the time the wood was formed, and the consequent proximity of the site of wood formation to the most physiologically active regions of the upper live crown.

The pattern of development with age of latewood characteristics (latewood percentage; maximum density and the associated intra-incremental density range; and the wall thickness (increase) and lumen diameter (decrease) of latewood tracheids); viz., a very steep gradient of change over the inner 6 to 8 growth rings from negligible or poor latewood development in the innermost 1 to 3 rings to well defined intra-incremental zones of very dense latewood tissue, and the subsequent gradual increase in latewood percentage and ring maximum density with age; results in a conspicuous juvenile core of light-textured wood of relatively low density (but generally not less than 0.4 g/cm^3 extracted

density). The central core is of considerable extent, as the radial growth rate during the period corresponding with corewood formation is relatively great. This feature of structural development could give rise to problems of seasoning degrade and variable strength properties caused by the inclusion of juvenile and mature wood in sawn material.

Phenotypic differences between trees in the absolute values of specific wood characters and in their patterns of variation within the stem are of an exceptionally high order: This is particularly evident in the extent and pattern of development of latewood characteristics, which reflect a high degree of between-tree variation of wood textural features.

Estimates of the value of individual wood characters derived from measures taken at a single height level between breast height and 60% (often 80%) of tree height were shown to be representative of the corresponding whole-tree values. Measures of samples taken at 20% of tree height closely approximate the whole-tree estimate, whilst measures of samples taken below and above this level overestimate and underestimate, respectively, the whole-tree value. The observation that valid between-tree comparisons can be made by sampling at a single level in the standing tree has important implications for the development of efficient small-scale sampling procedures.

An estimate was made of the effects upon the wood characteristics of radial growth rate and of position effects associated with height and age. A detailed discussion of the results and conclusions is presented in Section 4.5. Simple correlation analysis proved ineffective in estimating the relative influence of radial growth rate and position effects upon the development of specific wood characters, because the variation within individual stems of many of the wood characters and ring width is approximately collinear with that of ring age. The utility of simple correlation analysis in interpreting inter-relationships among the complex of wood characters (Section 4.2) was similarly restricted, because the magnitude of the coefficients of correlation may be influenced by the similarity of the axial and radial patterns of development of the different characters.

A principal component analysis proved effective in isolating orthogonal (statistically independent) vectors representing axial and

radial position, and radial growth rate. The variation of the densitometric characters and the closely associated variation of lumen width and wall thickness of the latewood tracheids was shown to be independent of radial growth rate, *per se*, but strongly associated with radial and axial position effects. In contrast, the lumen and cell widths of earlywood tracheids were not affected by position within the stem, and, together with the width of the intra-incramental latewood zone and the associated cell width of the latewood tracheids, were strongly influenced by radial growth rate.

The nutritional status of the soil and foliage was examined. The inter-relationships between individual nutrient factors and complexes of inter-related factors in the soil and foliage were identified and estimated. The between-tree component of variation of the wood characters was examined and the inter-relationships between the wood characteristics and nutritional features of the soil and foliage determined. A detailed discussion of the results and conclusions is presented in Section 4.7.

The relationships between the measured soil features and the wood characteristics of the trees were generally negligible or weak and poorly defined. Some relationship was evident between the anatomical characteristics of the earlywood tracheids and the measured soil features; a relationship most consistently associated with soil pH.

A moderately strong relationship between the foliage nutrient levels and the lumen and cell widths of the tracheids was shown; the strongest relationships involving these anatomical characteristics of the earlywood cells. The relationships effectively involve few of the foliage elements. Thus, the lumen and cell widths and the wall thickness of the earlywood tracheids show a close positive association with the foliage levels of calcium and potassium. The level of iron in the foliage is strongly associated with the lumen and cell diameters of the latewood tracheids, and foliar potassium shows a moderate positive association with these anatomical traits. Of the densitometric characters, minimum (earlywood) density shows some relation to the overall nutrient status of the foliage and is negatively related to the level of zinc in the foliage, and the width of the intraincremental latewood zone is positively associated with the level of

foliar iron; but the relationships of the other characters with the foliage nutrients are poorly defined.

The content of this thesis describes in detail an integral portion of a very much more comprehensive programme of research of the variation of wood characteristics of Queensland-grown var. *hondurensis* undertaken by the author. The programme included a similarly detailed analysis of the densitometric features of the wood, and estimates of variation in wood anatomy, of trees growing in trial plots established on sites of diverse nature in tropical and subtropical Queensland. These plots were from two geographic locations:

(a) Three trial plots established in 1954 (seed origin: Mt. Pine Ridge, British Honduras) at widely varying altitude in north Queensland (latitude approximately 17° 00' S). Ten trees from each plot were studied.

(b) Three trial plots of variable site index established in 1952 (seed origin: Batch 3; Mt. Pine Ridge, British Honduras) in the State forests at Toolara and Tuan in southern coastal Queensland (26° S). Six trees from each plot were studied.

The samples of wood, foliage, and soil were collected in December of 1971; one year subsequent to the collection of material from the Beerburrum planting.

Some results of the north Queensland study are presented in tabular and diagrammatic format in Appendix 3. Their detailed presentation is beyond the scope of this thesis, and the results of this extended research effort will be published independently at a future date.

Important influences of site factors upon growth and the characteristics of the wood formed in trees of var. *hondurensis* have been implicated in studies from the natural range [e.g., Hughes, 1970] and from exotic plantings. Considerable differences between stands in wood yield and average values of some structural characteristics [e.g., Smith, 1973], and in their patterns of development [e.g., Harris, 1973a] have been demonstrated.

A substantial element of the variation of structural characteristics of the wood from populations established on differing sites is known to be associated with marked differences in latewood development [see Harris, 1973a; Boone, Chudnoff, 1972; Smith, 1973]. The intra-incremental pattern of latewood development ranges from a variable number of narrow bands of latewood tissue interspersed with earlywood tissue ("false rings") to a single, well-defined latewood zone. The formative duration and extent of the central core of wood in which latewood is poorly developed or absent is known to vary quite markedly between trees [see Boone, Chudnoff, 1972]; but relationships between this developmental feature and site factors have not been defined.

Differences between sites in the amplitude and periodicity of soil moisture deficits have been suggested as likely critical factors influencing the pattern of latewood development [e.g., Hughes, 1970; Harris, 1973a; de Villiers, 1973]. But the environmental factors influencing soil moisture availability and cyclic growth behaviour involve complex interactions among climatic and soil variables that may vary in kind and degree between sites.

A comparison of the structural features of the wood from each of the stands growing at different altitudes in tropical north Queensland (17° 00' S) (Appendix 3) and the plantation at Beerburrum (27° S) reveals interesting similarities and differences. The trees are of comparable age and provenance.

Differences in stocking density, silvicultural history, and a complex of site factors including soil type and climate, complicate any generalised interpretation of the variation of wood structural features in terms of response to changes in altitude or latitude: The presentation of results from the north Queensland study (in Appendix 3) is intended to effect a summary of the extent and nature of the variation encountered; and no attempt is made at hypothetical inference.

The structural features of the wood differed significantly between each of the stands in north Queensland. A major aspect of the variation between plots is associated with the patterns of development in the stem and the magnitude of the intra-incremental density contrast.

These features are determined by the variation of ring maximum (latewood) density.

There are pronounced phenotypic differences between trees in the absolute value and the pattern of variation of maximum (latewood) density at each site (Figure A.1(b)) : Between-tree differences are greatest at Kuranda (altitude 460m (1500 ft) a.s.l.), where the range of maximum density is extraordinarily great (0.470 - 0.958: whole-tree weighted average values - Table A.3).

In the trees from each of the stands annual growth layers were distinctly separable into one major zone of latewood* and one of earlywood: The incidence of minor latewood bands ('false rings') of relatively low density in the 'earlywood zone' was variable but of a low order.

The wood from Danbulla (760 m: 2500 ft) is remarkably even-textured and of relatively low mean density. Density gradients outward from the pith are slight (Figures A.2, 3; Table A.3).

By contrast, in most trees at Kuranda (460 m: 1500 ft) (but c.f. tree 1) and in all trees at Mt.Sophia (15 m: 50 ft) maximum density increases abruptly outward from the pith to about the seventh growth ring: The gradient of whole-ring mean density increase over the corresponding period is steep also. This feature of structural development results in a very distinct core of juvenile wood: This core is of considerable extent, because of the very high radial growth rate during the period corresponding with corewood formation.

The growth responses of the trees show evidence of increased eco-physiological stress as the stand ages (from age about 9 years at Mt.Sophia and Kuranda; about 7 years at Danbulla - Figure A.6). In the Beerburrum planting there was no evidence of retardation of growth as the stand aged: But a comparative evaluation of growth response and related structural development in the wood, e.g., the relative proportion of corewood in stems, is complicated by the different stocking densities and silvicultural histories of the stands.

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* 'Latewood' tissue in some growth rings was difficult to distinguish visually in the wood from Danbulla.

Inter-relationships among the densitometric characters were examined, using the technique of principal component analysis. The inter-relationships among the characters are essentially similar in the wood from each of the northern plots and the Beerburrum material (Fig.A.5).

The effect of sample height upon the estimate of whole-tree values of each of the densitometric characters was examined in the trees from each stand. The results in each case confirm the conclusions derived from the study of the Beerburrum material; viz., that measures of samples of the stem cross-section taken at any given level from breast height to 60% of tree height provide estimates that are representative of whole-tree values and, thus, facilitate valid between-tree comparison. The disc average estimate at 20% of tree height very closely approximates the whole-tree average value (Tables A.4).

A wide variation of wood structural characteristics of var. *hondurensis* of Mt. Pine Ridge provenance is evident between stands established on sites of diverse nature in Queensland. These results confirm and extend the evidence from previous studies of a broad spectrum of response of wood characteristics in var. *hondurensis* to the influence of variable site factors. Little is known of the causal factors underlying this variation: Indeed the nature of the variation has rarely been precisely defined and is not well understood. But response of such magnitude to the influence of site factors has far-reaching implications for control of wood quality.

Very pronounced phenotypic differences between trees in important structural characteristics of the wood and their pattern of development are evident at all sites. The demonstration of between-tree differences of very considerable magnitude in a stand does not constitute absolute evidence of genotypic variation. But a significant element of variation of a heritable nature has been demonstrated in several important wood structural characters including tracheid length, latewood percentage [Squillace, Echols, Dorman, 1962], and wood density [see Zobel, 1970]; and it would seem reasonable to assume, from the extent of the between-tree differences demonstrated in this study, that progressive improvement of wood characteristics is possible through selection and breeding of trees with desirable characteristics.

Selection and breeding for wood quality presents practical problems in the selection of genotypes which have a desired wood property but retain the essential traits of vigour and stem straightness. The problems are exacerbated by difficulties in deciding which properties are desirable for processing and a variety of possible end uses, or will prove desirable in the future. Appropriate values associated with vigour and straightness are well known, but little information is available on values associated with wood characters: Namkoong, Barefoot, and Hitchings [1969] conclude that it is impossible for the tree breeder to decide how much effort to devote to changing wood properties.

Nevertheless, substantial change of specific wood characters is possible without sacrificing vigour [see Zobel, 1970]. The major variation in the densitometric features and latewood development in var. *hondurensis* was shown, in this study, to be independent of the effects of radial growth rate. To the extent that this pronounced variation is of a heritable nature, manipulation of wood characteristics by selection and breeding should prove effective.

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APPENDIX 1

PRINCIPAL COMPONENT ANALYSIS

Multivariate statistical techniques are defined as those which analyse simultaneously the variation and covariation among several quantitative characteristics. Principal component analysis (PCA) is a metric model, which, in its modern form, is due to Hotelling [1933]. No assumptions or constraints are placed upon the structure of the multivariate sample space or upon the distribution of variables within it; i.e., PCA is an "internal" analytical technique [Bartlett, 1950], demanding no *a priori* knowledge of the structure of the sample.

The technique is one of deriving orthogonal (independent) linear combinations of a set of p correlated responses on n observations so that the variance of each such combination, taken in turn, is maximised. The mathematical derivation of the PCA model is described in detail elsewhere [Quenouille, 1952; Kendall, 1957; Seal, 1964; Morrison, 1967; Cooley and Lohnes, 1971].

Geometrically, the method consists of locating the principal axes, in order of magnitude, of the multivariate sample space. This is achieved by rotation of the p axes of the original co-ordinate system to new orthogonal axes (principal axes), so that the variability of the n original sample points projected onto the first principal axis (as measured by the sum of squares of the projected points) is greatest. The second axis is chosen, orthogonal (i.e., at right angles) to the first, such that the variability along this axis is next greatest, giving maximum scatter in the plane formed by the two (orthogonal) axes, and so on. There are p such axes unless either: (i) there is a complete linear dependence between two or more of the variables, or, (ii) the number of variables is equal to or greater than the number of observations, in which case a sample space of (n-1) dimensions and principal axes is defined.

In practice, if R is a $(p \times p)$ correlation matrix, where p is the number of variables, principal component analysis requires the

calculation of the eigenvalues (λ_ℓ) and corresponding eigenvectors (a_ℓ) of R.

The eigenvalues, λ_ℓ, of the correlation matrix, R, are extracted in descending order of magnitude. The eigenvalues, λ_1, λ_2, λ_3, etc., represent respectively the largest, second largest, third largest, etc., axes of the standardised multivariate sample space.

The eigenvectors, a_ℓ, corresponding with each root, define a new variable or principal component

$$z_{i\ell} = \sum_{j=1}^{p} y_{ij} \cdot a_{j\ell}$$

(where y_{ij} is the standardised value of the j^{th} variable in the i^{th} observation) which has a variance of λ_ℓ, the eigenvalue. Thus, the eigenvectors provide the coefficients which define the principal components, or linear combinations of the original variables.

The principal components, z, have two distinct properties: They are uncorrelated one with the other; and they may be arranged in descending order of variance, each successive z having the maximum possible variance after removing the contribution of previous z's to the matrix, R. The corresponding eigenvalues, λ, the variances of the principal components, provide a measure of the proportion of the total variation accounted for by each component.

Although it is possible to extract as many vectors as there are variables (p), the number may be reduced substantially by deleting those with the smaller variances (λ). This, in effect, reduces the number of variates with a minimal discard of information; so allowing the problem to be viewed in a reduced number of dimensions, with minimal distortion. Bartlett's test of significance of the roots [Bartlett, 1950] has been applied, but is of relatively little value since all the roots may prove to be statistically significant. Deletion of vectors is thus largely a subjective process; but the information discarded, although not non-significant in the statistical sense, is difficult to interpret in the context of interrelationships among the attributes represented by the original variables.

The eigenvector coefficients can be used as scores, indicating the relative contribution of the variables to any given principal

component. Comparison of scores between principal component vectors is facilitated by the scale transformation

$$f_{\ell j} = \lambda^{\frac{1}{2}} a_{\ell j} .$$

Scaling is necessary, since each vector is associated with a different variance (as measured by its eigenvalue, λ). The f-values, or factor loadings of the variables on the components, are coefficients of correlation between each variable and the principal component.

The f-values may be used to ordinate† the variables on the principal components. This is achieved by arranging the variables in descending order of the elements (factor loadings, f) in the first principal component vector.

TRANSFORMATIONS

In the most rigorous form of PCA it is assumed that the variates are continuous, linearly related to one another, and normally distributed; i.e., that they are drawn from a multivariate normal population [Seal, 1964, p.170]. The effects of departure from model and assumptions are discussed in detail by Cassie [1968, 1972].

It should be noted that the estimates of the population parameters corresponding with the derived statistics (correlation coefficients, eigenvalues, eigenvectors) become increasingly uncertain as departure from multivariate normality increases. Statistical inferences from subsequent operations, such as regression or correlation analysis, are valid only if the distribution of the original variates has been specified.

The conditions of linearity and normality (or at least relative symmetry) of the frequency distributions of the variables may be approximated by the use of transformations.

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† Arrangement in a multidimensional series [Goodall, 1954].

APPENDIX 2

LABORATORY ANALYSES OF FOLIAGE AND SOIL SAMPLES

1. FOLIAR CHEMICAL ANALYSIS

(a) Sample Preparation

Foliar samples were dried at 30 °C in a forced air flow, and ground finely in a grinding mill, then dried at 85 °C for 12 hours and cooled in a desiccator over silica gel. Two subsamples of 0.2 g and 0.4 g respectively were taken at random and weighed to an accuracy of 0.001 g.

(b) Analytical Procedures

The levels of nitrogen and phosphorus were determined from the smaller (0.2 g) subsample, and the concentrations of the cations calcium, magnesium, sodium, potassium, iron, zinc, and manganese were analysed using the 0.4 g subsample.

(i) Nitrogen and phosphorus

The levels of nitrogen and phosphorus were determined using a slight modification of the technique described in detail by Williams and Twine [1967].

The samples were digested at 250 - 280 °C in a mixture of potassium sulphate (200 g) and selenium powder (1 g) dissolved in concentrated sulphuric acid (1 ℓ). Colorimetric measurements were made simultaneously for both N and P on a twin channel Technicon autoanalyser.

Phosphorus was measured as the absorbance of the intense blue complex, "molybdenum blue", formed by ascorbic acid reduction of the phospho-molybdate complex formed from ammonium molybdate and sample phosphorus. Absorbance was measured at 660 mμ.

Total nitrogen was determined by a modified Kjeldahl method using alkaline phenate and sodium hypochlorite. Absorbance was measured at 625 mμ.

(ii) Cations

The concentrations of the cations were determined by atomic absorption spectrophotometry [Walsh, 1956, 1963; Willis, 1963].

The samples were digested at 250 - 280 °C in 5 ml of a ternary acid mixture comprising concentrated sulphuric acid (1 part), perchloric acid (7 parts), and nitric acid (24 parts). Digestion was followed by filtration, appropriate dilution, and measurement of absorbance.

Excess magnesium in the form of a final solution concentration of 2% H_2SO_4 and 6000 ppm Mg was used to suppress interference effects of phosphorus (aluminium in soils) in the determination of calcium levels. For magnesium determination an excess of lanthanium oxide was added during dilution to suppress interference.

(iii) Computation of sample nutrient levels

Graphic output from the autoanalyser was converted to digital net peak height measures by hand measurement. Output from the atomic absorption spectrophotometer was in digital form.

Elemental concentrations were calculated from these data using a programme, "PEANUTS", developed by A.V. Spain [Spain, 1970]. The programme fits a second degree polynomial regression of the estimates of transmission or peak height on the concentrations of the standard solutions. The regression equation is solved for the independent variable to obtain, by interpolation, the elemental concentration of the solution of each sample.

2. SOIL CHEMICAL ANALYSIS

(a) Sample Preparation

The soil samples were spread on paper and dried at 30 °C in a forced air flow. Litter and root material were removed, and the air-dry soil was rolled gently to disrupt the coarser structural elements (granules, etc.) and passed through a 1 mm sieve.

A subsample was extracted for determination of soil pH. The remainder of each sample was dried at 85 °C for 12 hours and cooled in a desiccator over silica gel. Two subsamples were taken at random and accurately weighed (to 0.001 g) for determination of soil chemical levels. A subsample of 6 g was taken for determination of % loss on ignition.

(b) Analytical Procedures

(i) Soil pH

Two 10 g subsamples of air-dry soil were each suspended in 25 ml distilled water, shaken vigorously, and left to stand for 10 hours. Each subsample was again shaken vigorously immediately prior to each of two pH readings taken 5 minutes apart. pH was determined using a glass-calomel electrode pH meter. The sample pH was taken as the mean of the 4 readings.

Variation of the soil pH measure with the method of sample preparation is discussed in detail by Jackson [1962]. The soil:water ratio of 1:2.5 consistently provides excess water. This results in a reduction of the variation of the pH measure with variation in the water content of the suspension.

(ii) Nitrogen and phosphorus

The nevels of N and P were determined on subsamples of 0.5 g or 1.0 g, using the techniques described for foliar analysis.

(iii) Cations

The total levels of the cations Ca, Mg, Na, K, Fe, Zn, and Mn were determined from subsamples of 0.5 g using the techniques described for the analysis of foliar cations. Techniques rather similar to those used in the determination of Ca, Na, K, and Mg are described in greater detail by David [1960].

(iv) Loss on ignition

A subsample of oven-dried soil of approximately 6 g was accurately weighed, ignited in a muffle furnace at 550 - 600 °C for 120 minutes, cooled in a desiccator over silica gel, and reweighed. % loss on ignition was calculated as the percentage loss of weight of the oven-dry sample on ignition at 550 - 600 °C for 120 minutes.

3. ACCURACY OF ESTIMATE

The measures of the levels of each element in each of the foliage and soil sample units were made on duplicate subsamples. For each sample unit, the results from the two subsamples were compared, and their difference (expressed as a percentage of their mean value) was referred to a predetermined* scale (presented below) of acceptable limits for each foliage and soil element. In the rare instance of the difference exceeding the predetermined level, the measurement of the element was repeated.

The accepted levels of difference (%) between the measures of individual soil and foliage elements were:

Element	Foliage sample	Soil sample
Nitrogen	5	5
Phosphorus	2	2
Calcium	2	2
Magnesium	2	2
Potassium	2	2
Sodium	10	10
Iron	2	10
Manganese	2	10
Zinc	2	2

The level of each element in the sample unit was taken as the mean of the subsample values.

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* The accepted levels of difference between measures in subsamples of the sample unit were chosen to correspond with the highest levels of accuracy to be expected (from extensive experience) in the routine application of the analytical procedures used [F.J. Darlington, pers. comm.].

APPENDIX 3

WOOD FEATURES AND GROWTH OF TREES FROM THREE TRIAL PLOTS IN NORTHERN QUEENSLAND (APPROXIMATE LATITUDE 17°S)

The content of this Appendix presents a concise quantitative record of the magnitude and patterns of variation of a series of wood characters in trees of var.hondurensis growing on 3 sites at widely varying altitude in North Queensland. The data are extracted from the results of a study quite separate from the research effort described in the main body of the thesis, and as yet unpublished. They are presented to effect some indication of the extent and nature of variation of the wood features of trees of var.hondurensis of comparable provenance (Mt.Pine Ridge) and age (established 1954) grown in plantations on sites of diverse ecology. These data are intended to facilitate comparative discussion (see General Discussion; Chapter 5) : The nature of variation of wood features in exotic plantings of var.hondurensis established on diverse sites has rarely been defined precisely, and comparative data for Queensland-grown material is not available elsewhere.

Table A.1: Stand locations and characteristics.

Plot number	Plot location	Altitude (a.s.l.)	Stand characteristics
1	Mt. Sophia (near Gordonvale). Farm plot of Messrs J.N. and J.F. Hesp	15 m (50 ft)	67 trees of var. *hondurensis*: spacing 2.7 m × 2.7 m. Adjacent plantings of broadleaf species.
2	Kuranda (Black Mt. Road). Plot 9; Expt. 162 (R1073)	460 m (1500 ft)	70 × 10 rows. 650 stems per hectare
3	Danbulla. Plot 2; Expt. 265 (S107/3031)	760 m (2500 ft)	Approx. 99 trees. 1087 s.p.ha.

Table A.2: Average monthly rainfall (mm).

Plot	Interval of measurement	Month of the year												Annual average
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
1. Mt. Sophia	1882 - 1957	421	422	460	264	110	72	39	42	43	50	98	203	2225
2. Kuranda	1896 - 1963	423	389	435	233	106	77	48	42	37	42	70	164	2068
3. Danbulla	1922 - 1964	316	407	320	119	57	59	35	29	29	26	68	150	1614

Table A.3: Parametric estimates (plot means, between-tree ranges (in brackets), and standard deviations) of the weighted whole-tree average values of six densitometric characters from each of three plots.

Wood character	Mt. Sophia		Kuranda		Danbulla	
	mean	s.d.	mean	s.d.	mean	s.d.
Maximum density	.861	.089	.788	.146	.584	.027
	(.724 - .975)		(.470 - .958)		(.480 - .762)	
Minimum density	.317	.029	.315	.032	.325	.025
	(.272 - .358)		(.258 - .355)		(.285 - .364)	
Mean density	.514	.046	.478	.061	.426	.040
	(.447 - .586)		(.343 - .564)		(.377 - .493)	
Intra-incremental density range	.543	.071	.472	.119	.259	.077
	(.429 - .625)		(.212 - .607)		(.163 - .432)	
Latewood percentage	37.5	9.82	28.1	10.0	20.5	12.8
	(24.8 - 54.3)		(5.6 - 38.6)		(9.1 - 42.0)	
Width of the intra-incramental latewood zone	2.02	0.62	1.54	0.79	0.90	0.59
	(1.26 - 3.25)		(0.22 - 2.89)		(0.28 - 1.69)	

Table A.4: The effect of sample height upon the estimate of the whole-tree weighted average value of ring mean density (cf., Tables 4.12; page 105, for format and notation).

Plot 1: Mt. Sophia

whole-tree weighted value

mean	s.d.	s.e.
.514	.046	.015

Height in tree	x_{DW}	s.d.	$r_{x_{DW} \cdot x_{TW}}$	s.e.	Regression line			Regression coefficient s.e.
					equation	s.e.	F	
Breast height	.551	.063	.923 ***	.146	y = .14 + .68 x	.007	40.2 ***	.040 ***
10%	.534	.041	.952 ***	.116	y = -.06 + 1.08 x	.006	67.7 ***	.049 ***
20%	.520	.048	.928 ***	.141	y = .04 + .91 x	.007	43.6 ***	.052 ***
40%	.491	.055	.922 ***	.146	y = .14 + .77 x	.007	39.8 ***	.046 ***
60%	.499	.055	.691 *	.273	y = .22 + .59 x	.014	6.4 *	.087 ***
80%	.491	.038	.929 ***	.140	y = -.04 + 1.13 x	.007	43.9 ***	.064 ***

Plot 2: Kuranda

whole-tree weighted value

mean	s.d.	s.e.
.478	.061	.019

Height in tree	x_{DW}	s.d.	$r_{x_{DW}.x_{TW}}$	s.e.	Regression line			Regression coefficient s.e.
					equation	s.e.	F	
Breast height	.497	.060	.936 ***	.124	y = -.001 + .96 x	.008	57.1 ***	.045 ***
10%	.485	.070	.989 ***	.052	y = .06 + .86 x	.003	356.3 ***	.016 ***
20%	.479	.055	.959 ***	.100	y = -.03 + 1.07 x	.006	92.6 ***	.039 ***
40%	.467	.072	.971 ***	.085	y = .09 + .83 x	.005	131.2 ***	.026 ***
60%	.467	.066	.956 ***	.104	y = .07 + .88 x	.007	84.8 ***	.034 ***
80%	.460	.071	.846 **	.188	y = .14 + .73 x	.012	20.2 **	.057 ***

Plot 3: Danbulla

whole-tree weighted value

mean	s.d.	s.e.
.426	.040	.013

Height in tree	x_{DW}	s.d.	$r_{x_{DW} \cdot x_{TW}}$	s.e.	Regression line			Regression coefficient s.e.
					equation	s.e.	F	
Breast height	.454	.053	.969 ***	.088	y = .10 + .72 x	.004	122.0 ***	.023 ***
10%	.446	.046	.930 ***	.130	y = .07 + .81 x	.005	51.2 ***	.040 ***
20%	.426	.047	.922 ***	.137	y = .09 + .79 x	.006	45.2 ***	.041 ***
40%	.411	.039	.904 ***	.151	y = .05 + .92 x	.006	36.0 ***	.054 ***
60%	.409	.039	.827 **	.199	y = .09 + .83 x	.008	17.4 **	.071 ***
80%	.395	.036	.726 *	.243	y = .11 + .81 x	.010	8.9 *	.096 ***

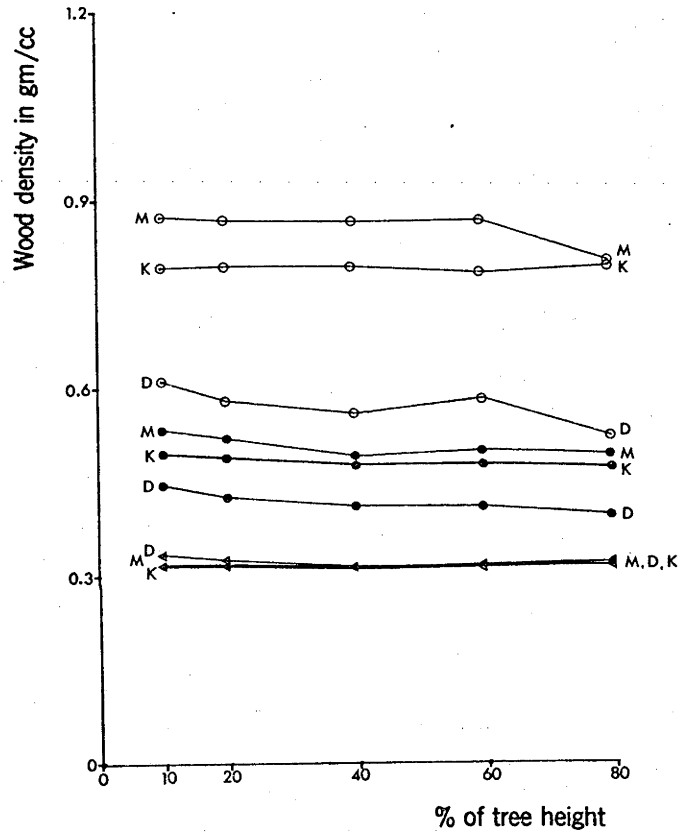
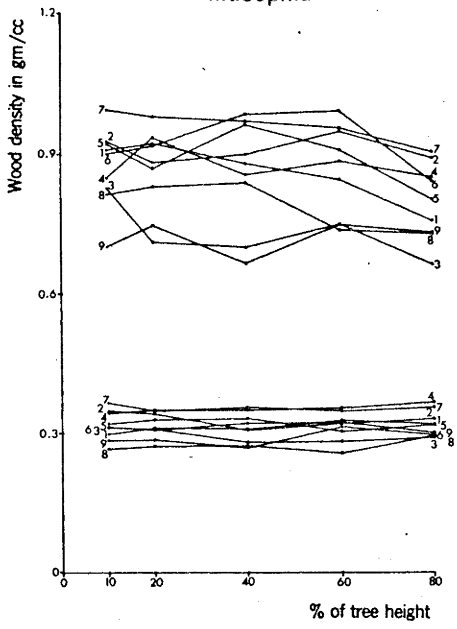


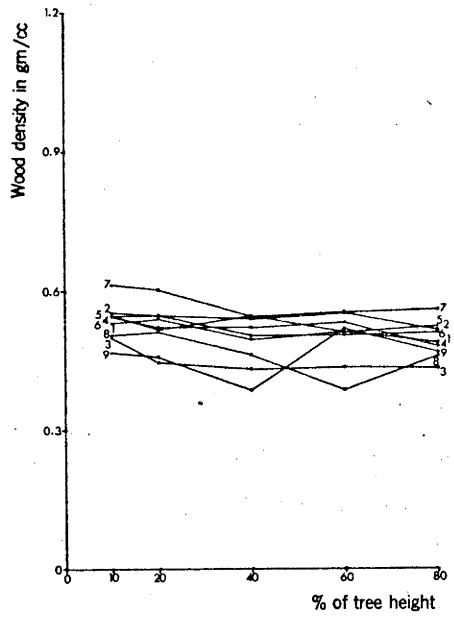
Figure A.1: Variation of the weighted average values of ring maximum, minimum, and mean density of the stem cross-section with height.

(a) Mean estimates from the pooled data of 10 trees from each of the plots: Mt. Sophia (M), Kuranda (K), and Danbulla (D).

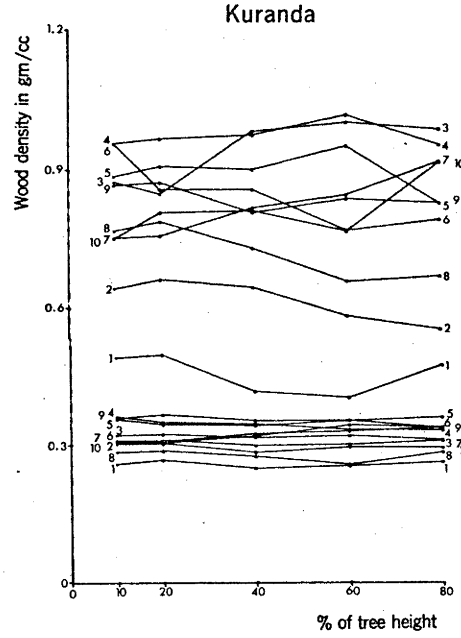
(b) (over page) In individual trees (numbered) from the plots at Mt. Sophia, Kuranda, and Danbulla.

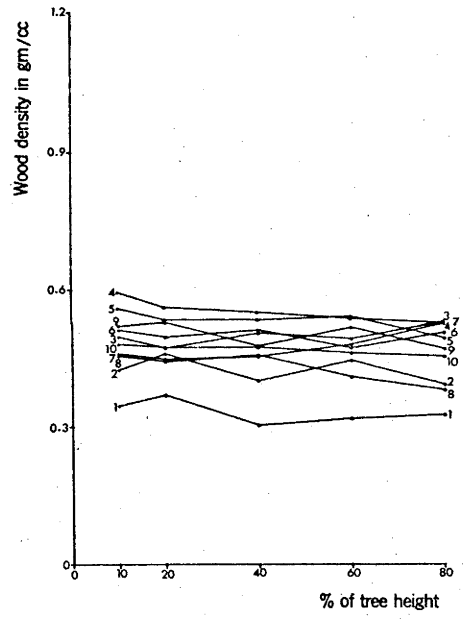
Mt.Sophia



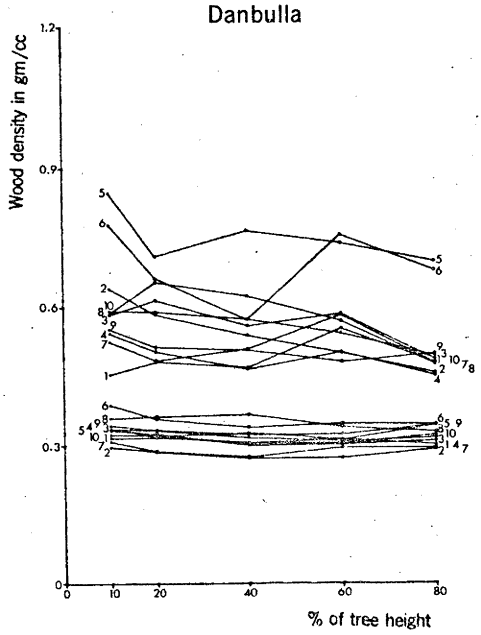


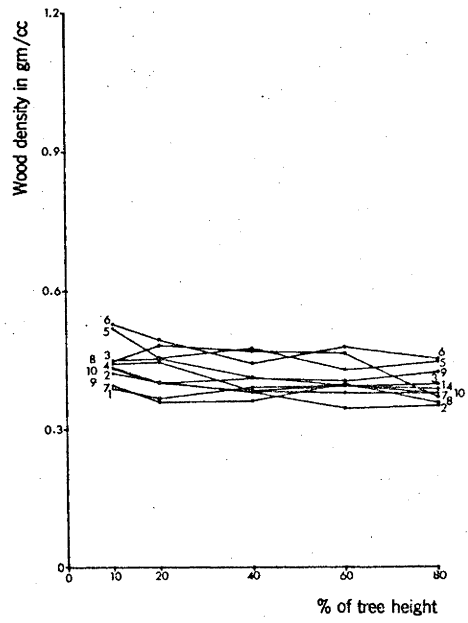
Kuranda





Danbulla





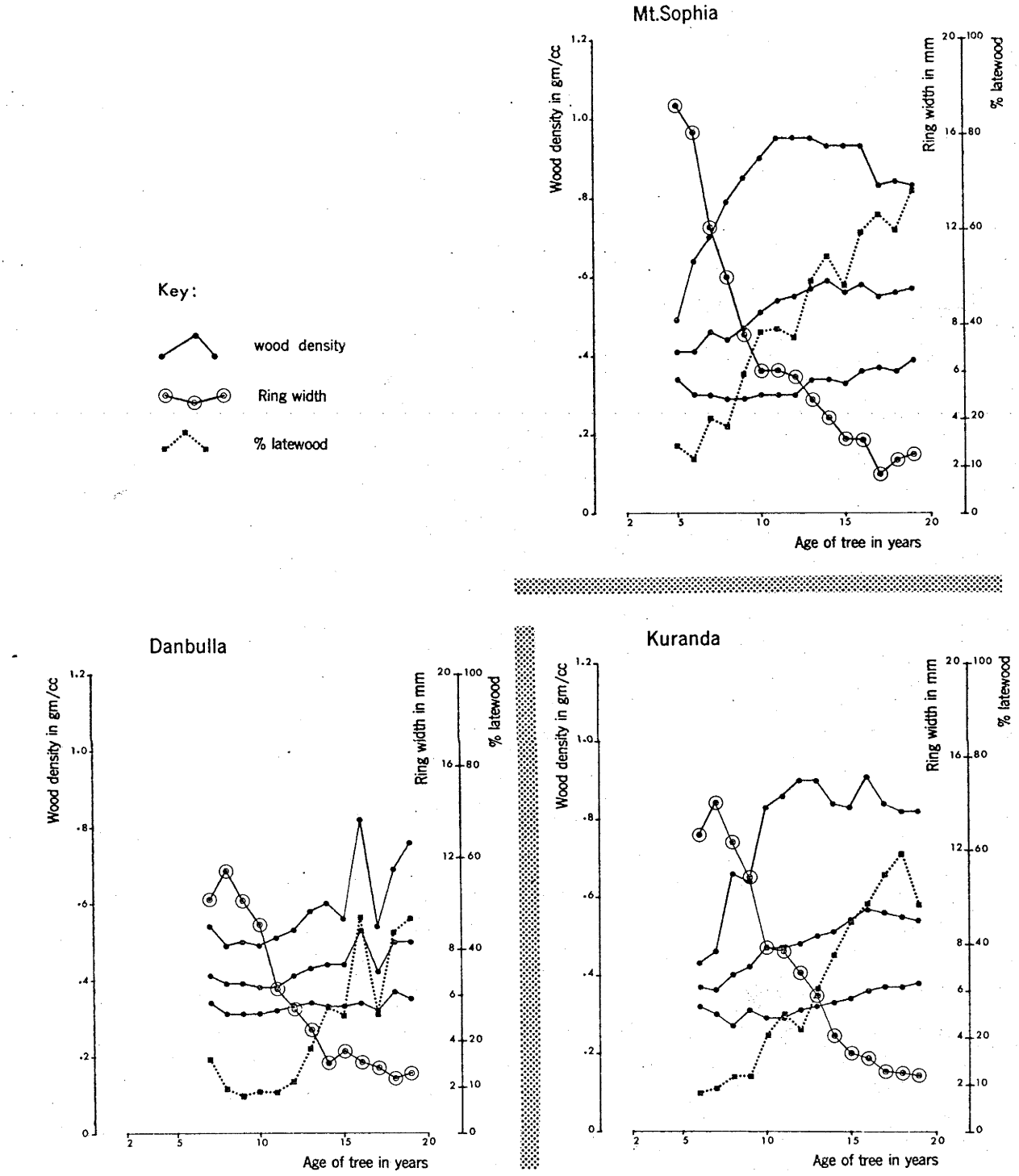


Figure A.2: The horizontal variation of wood densitometric features (maximum, minimum, and mean density; latewood percentage; ring width) of successive annual growth increments at 20% of total tree height. Each point on the curves represents the pooled data of the corresponding annual growth increments (measured from the bark) of 10 trees from each of the 3 plots.

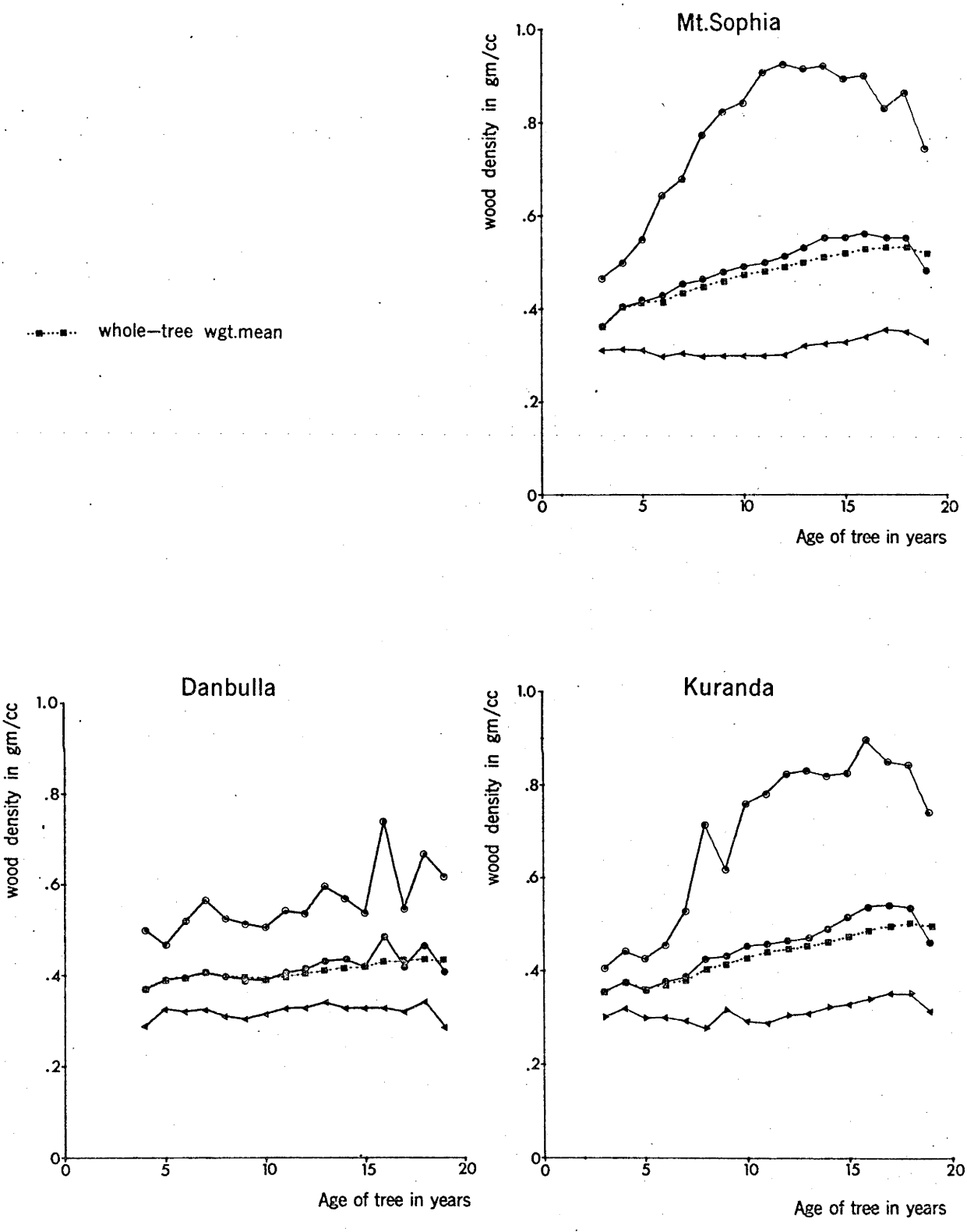


Figure A.3: The variation of the pooled estimates of the weighted values of maximum, minimum, and mean density of the wood of successive annual growth sheaths, and of the weighted whole-tree value of wood mean density in relation to tree age. Each point on the curves represents the simple arithmetic mean of the value at corresponding ages in 10 trees from each of the plots.

Figure A.4: The variation with age of the weighted estimates of maximum, minimum, and mean density of the wood of each annual growth sheath in individual trees from each of the 3 plots:

(a) Mt. Sophia (Plot 1).

(b) Kuranda (Plot 2).

(c) Danbulla (Plot 3).

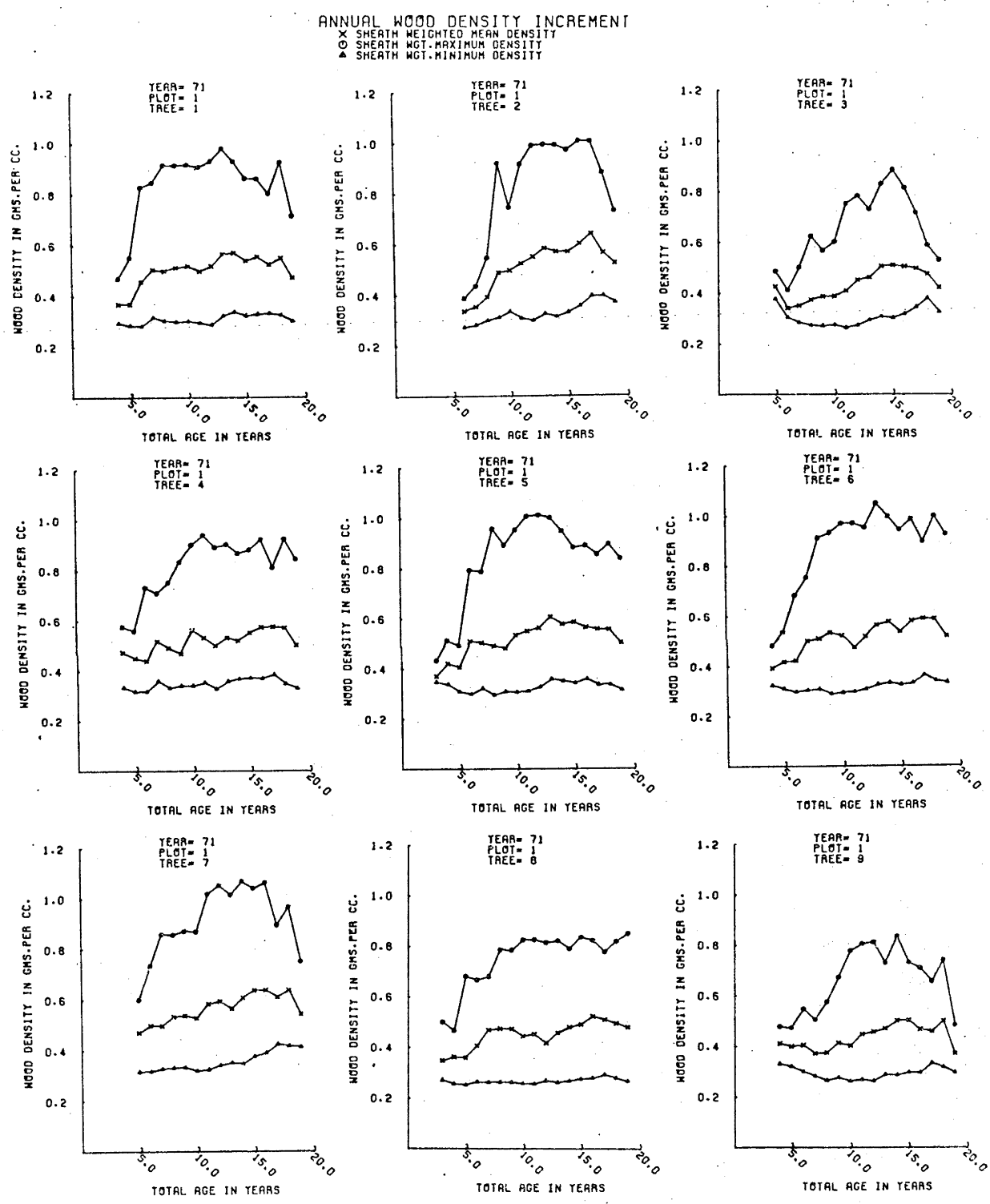


Figure A.4(a): Mt. Sophia.

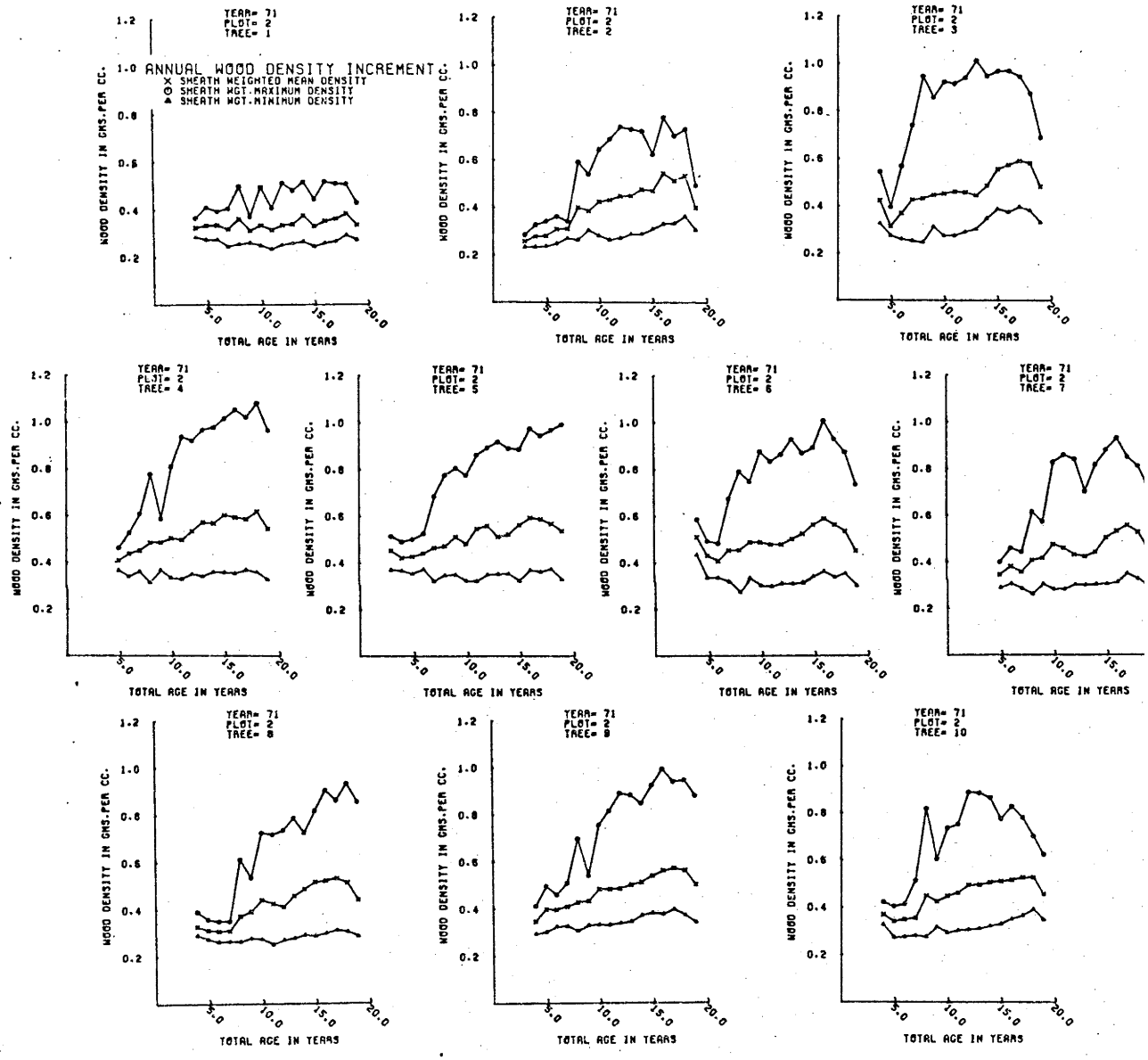


Figure A.4(b): Kuranda.

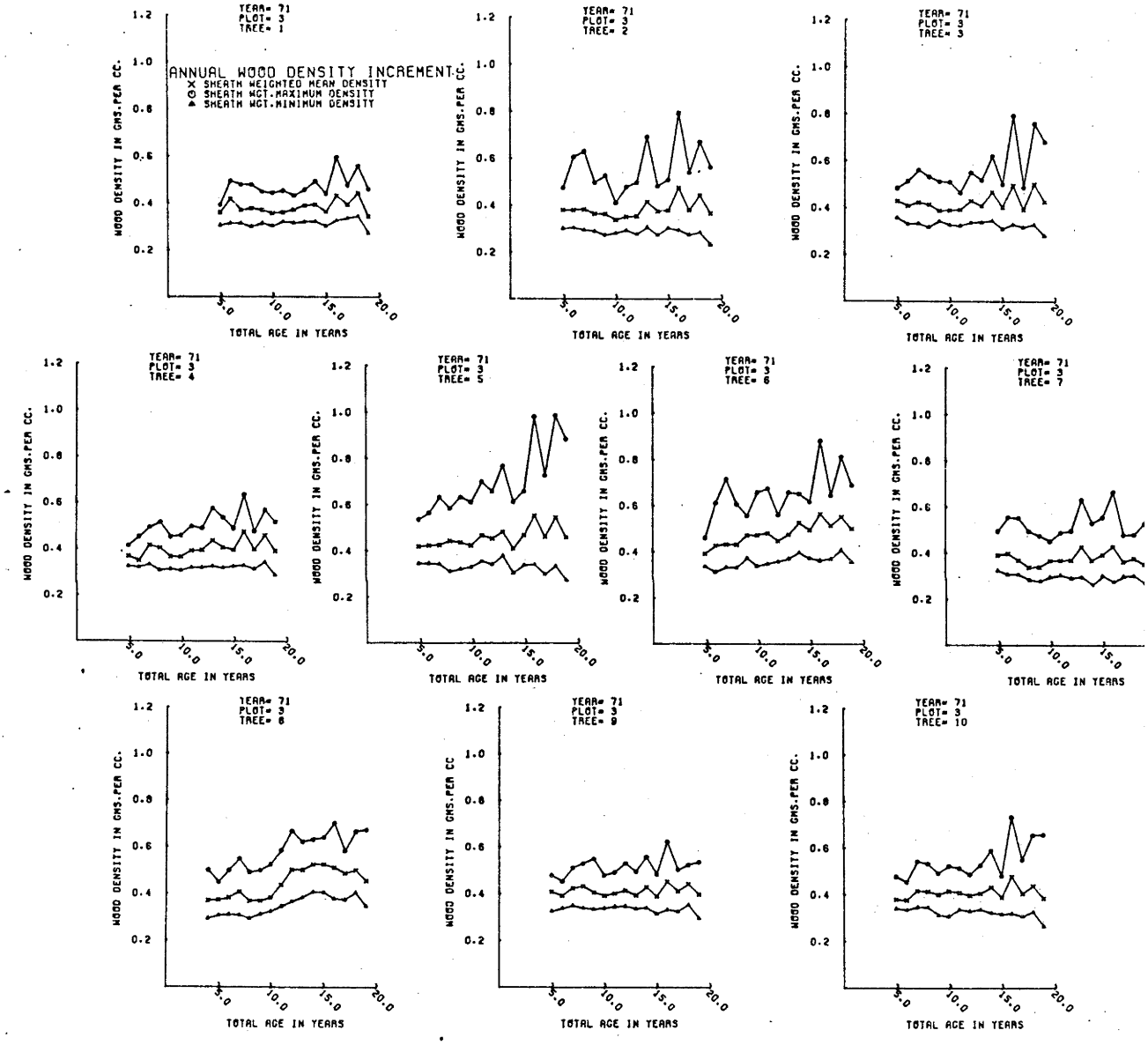


Figure A.4(c): Danbulla.

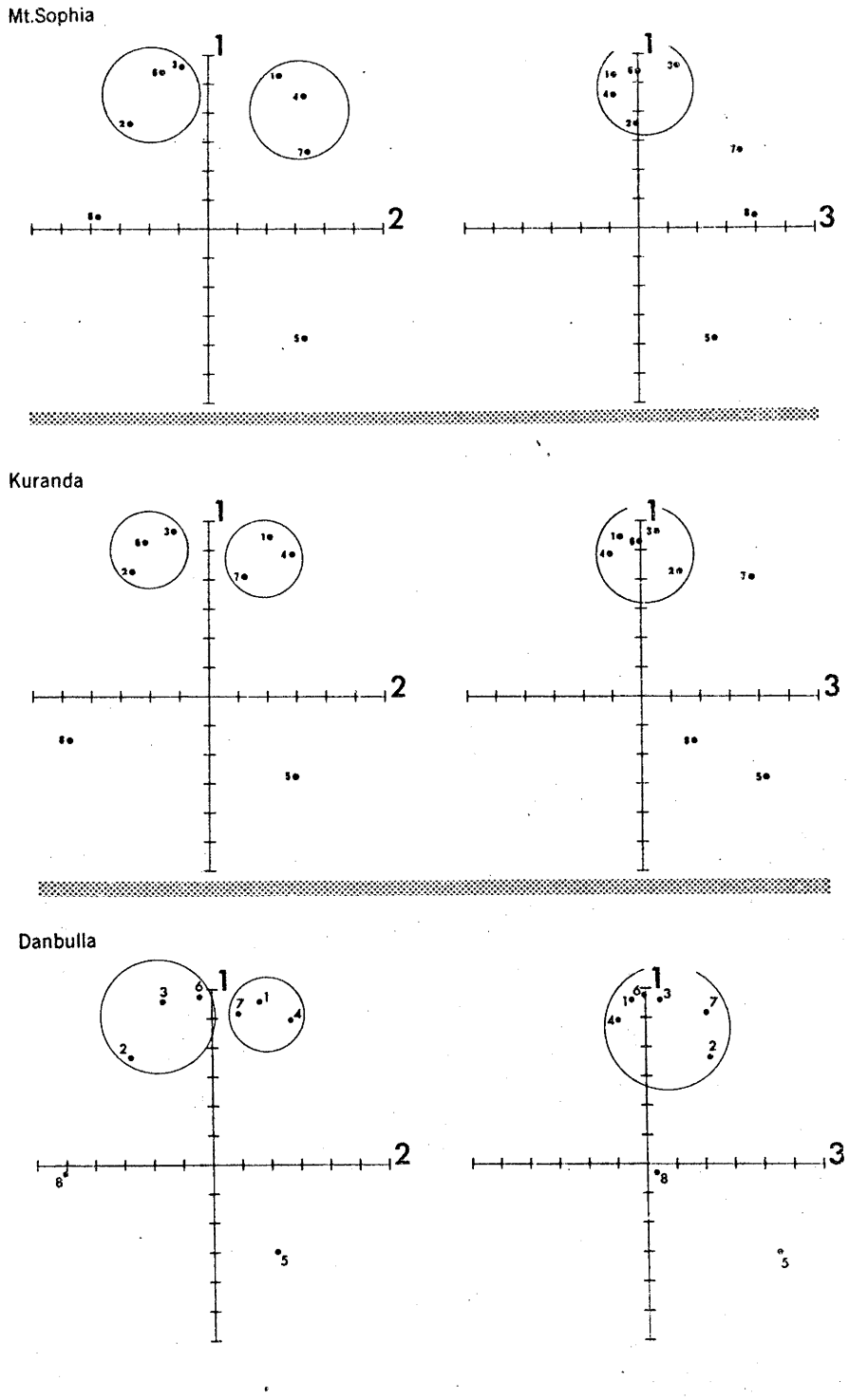


Figure A.5: Scatter diagrams of the wood character variables (numbered as in the main text: Table 4.1) on the main principal components extracted from the standardised values (pooled data from each plot) of 8 densitometric characters.

The co-ordinates of each variable are the factor loadings on the respective components. Each axis is scaled to unit length, so the co-ordinates of each variable represent the magnitudes of the coefficients of correlation between the variable and the respective components.

Figure A.6: Stem analysis figures: A graphical summary of the variation in growth patterns of the annual increment with age in individual trees from each of the plots:

(a) Mt. Sophia (Plot 1).

(b) Kuranda (Plot 2).

(c) Danbulla (Plot 3).

Mt.Sophia

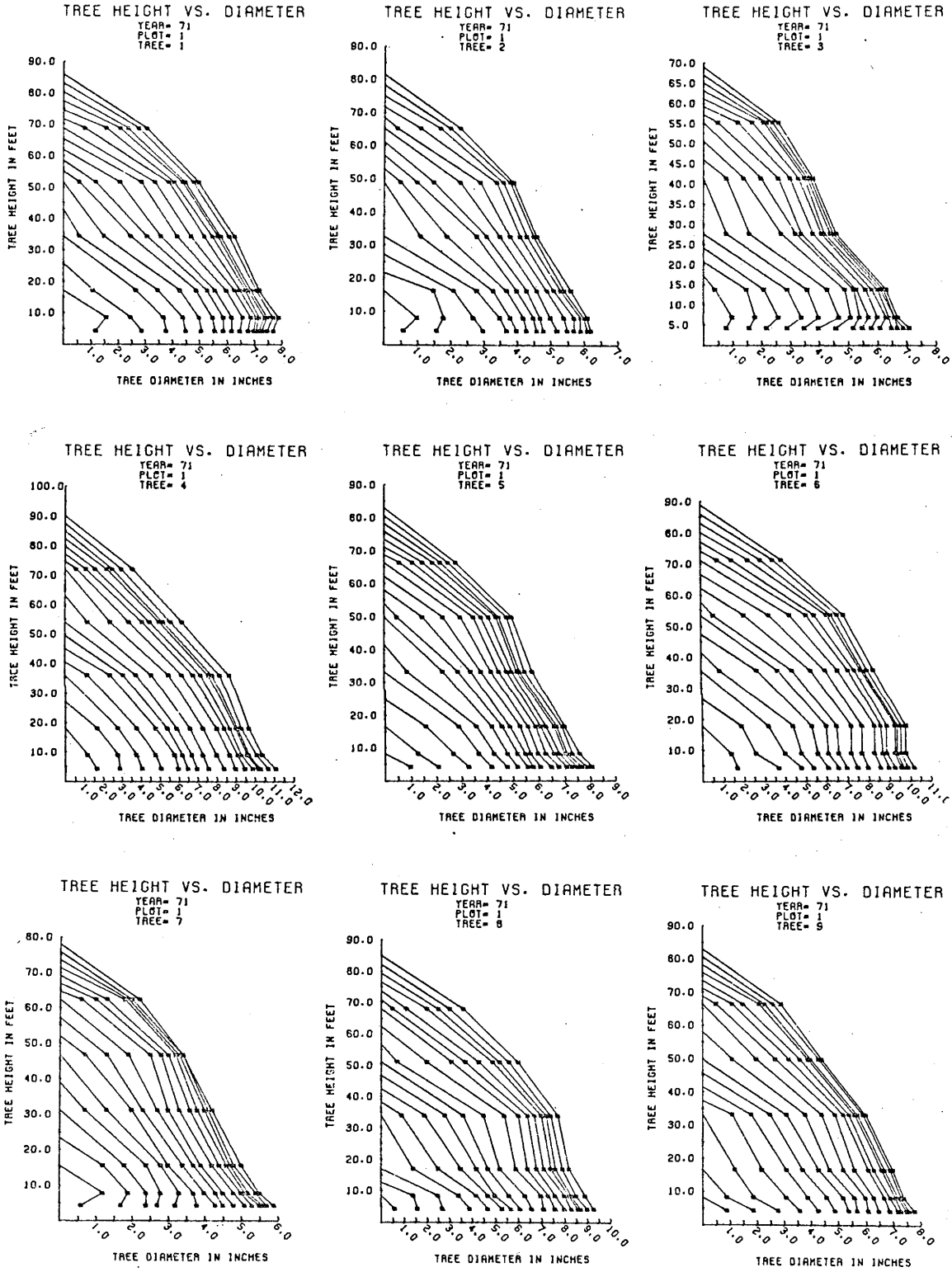


Figure A.6(a): Mt. Sophia.

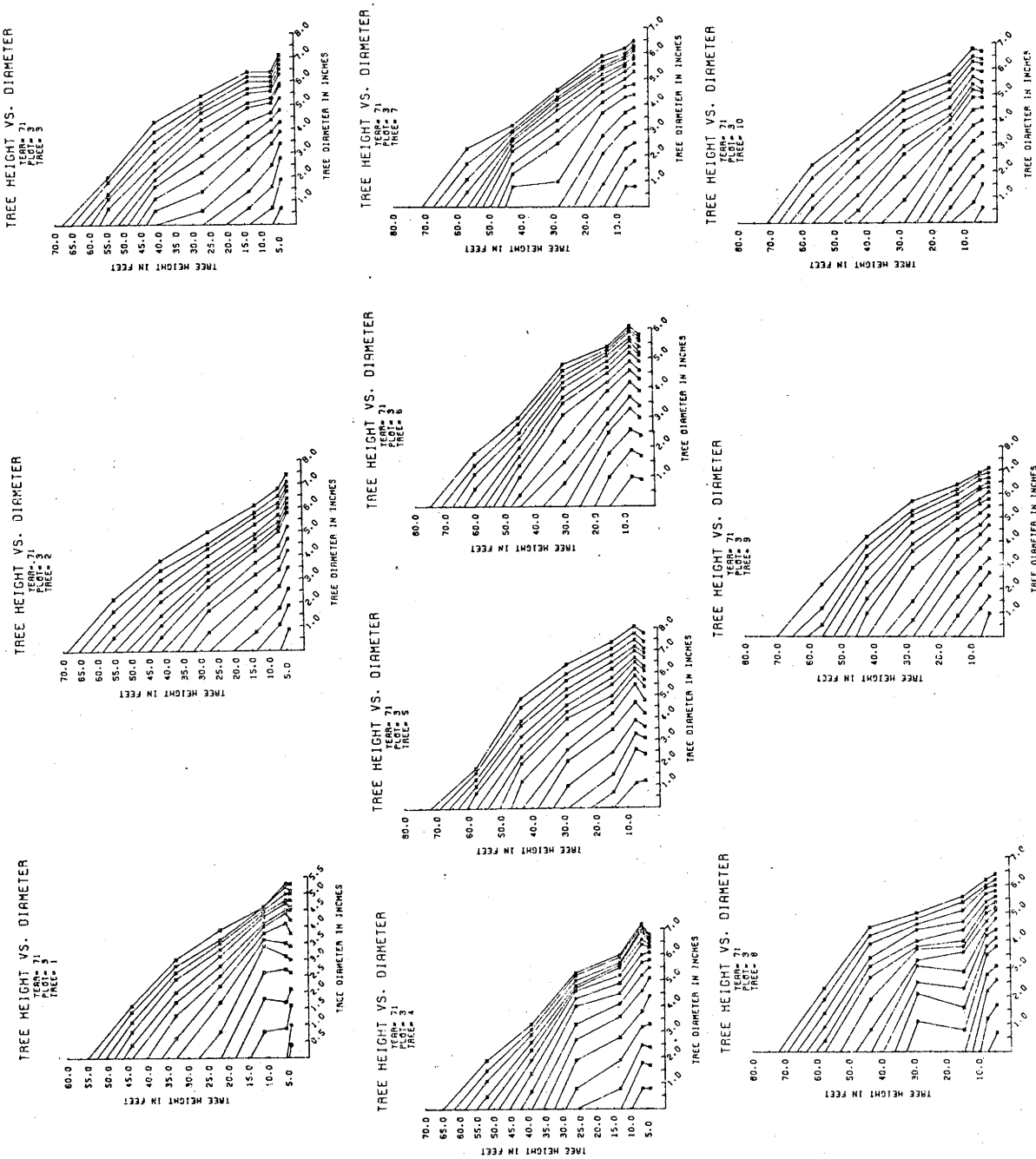


Figure A.6(c):
Danbulla.

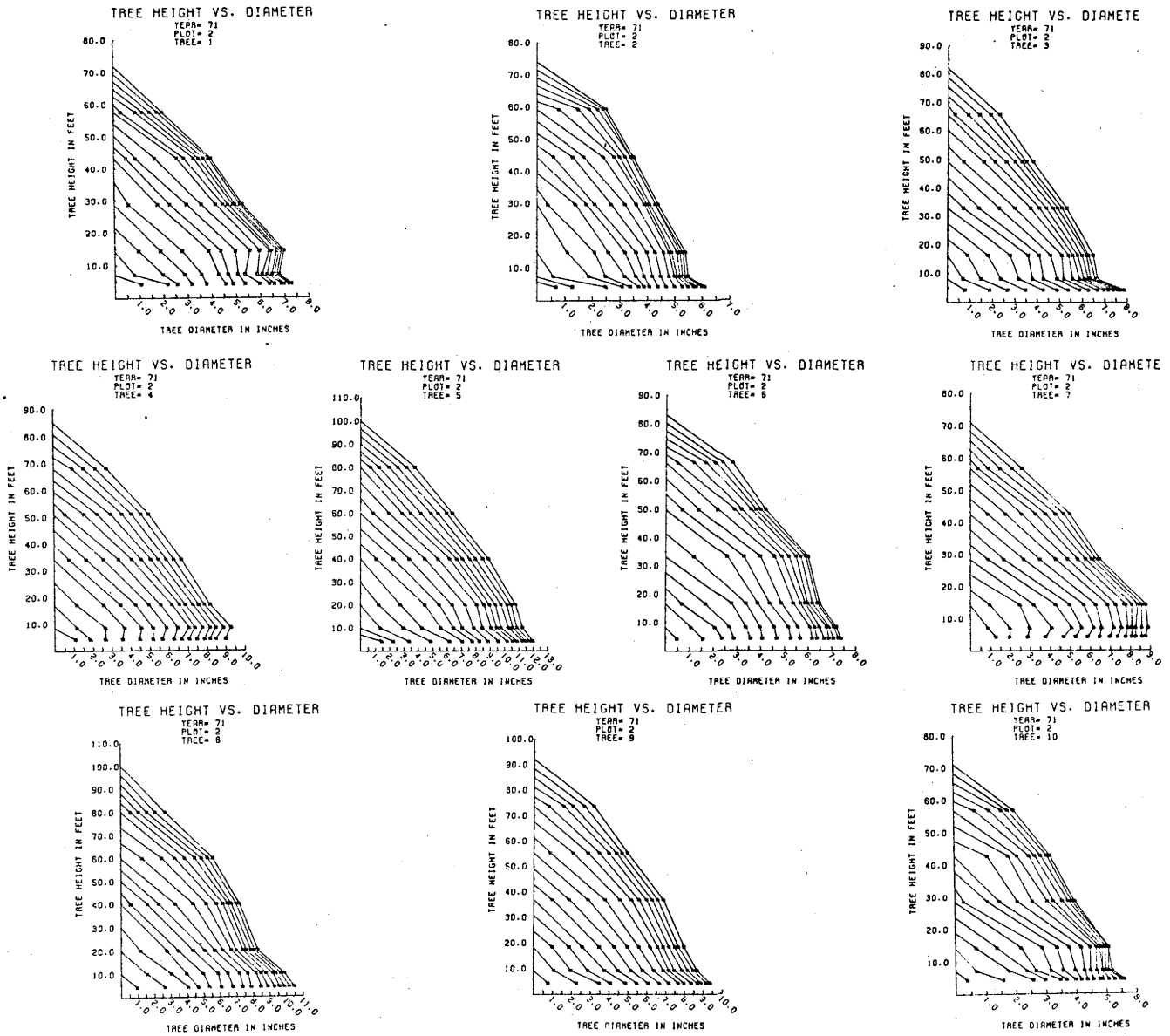


Figure A.6(b): Kuranda.

Figure A.7: Stem volume increment (x - mean annual increment; o - current annual increment) of individual trees from each of the plots:

(a) Mt. Sophia (Plot 1).

(b) Kuranda (Plot 2).

(c) Danbulla (Plot 3).

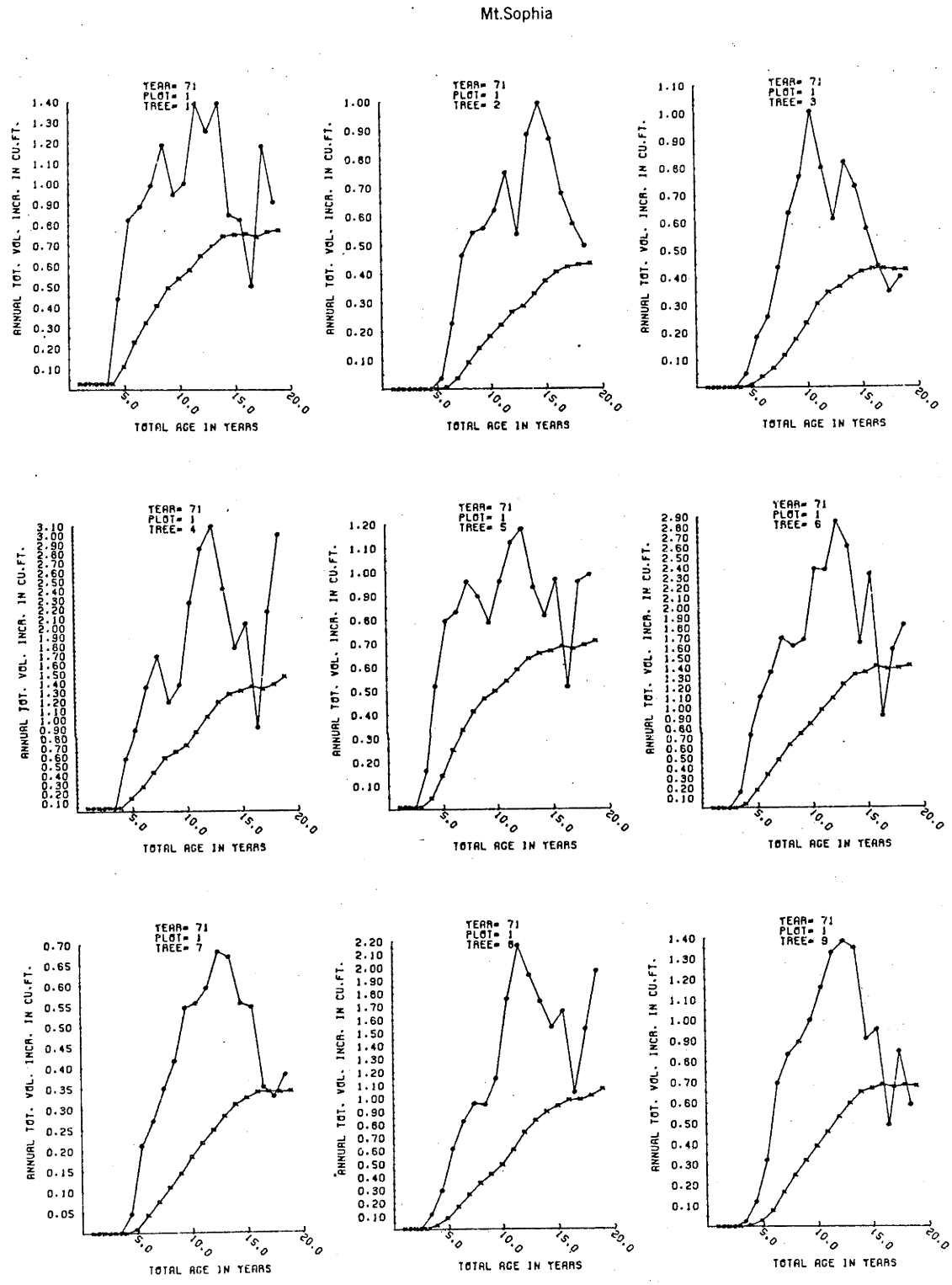


Figure A.7(a): Mt. Sophia.

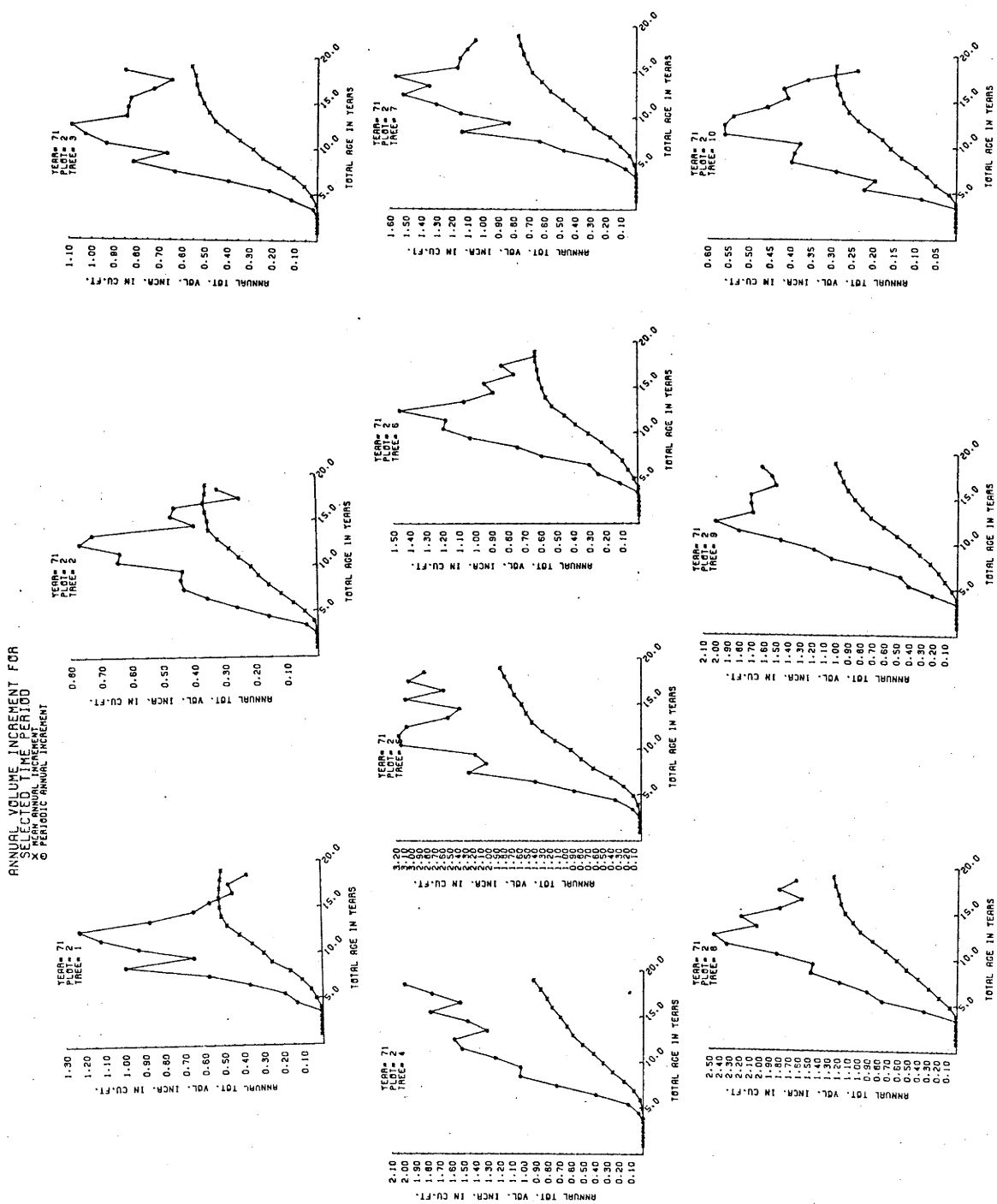


Figure A.7(b):
Kuranda.

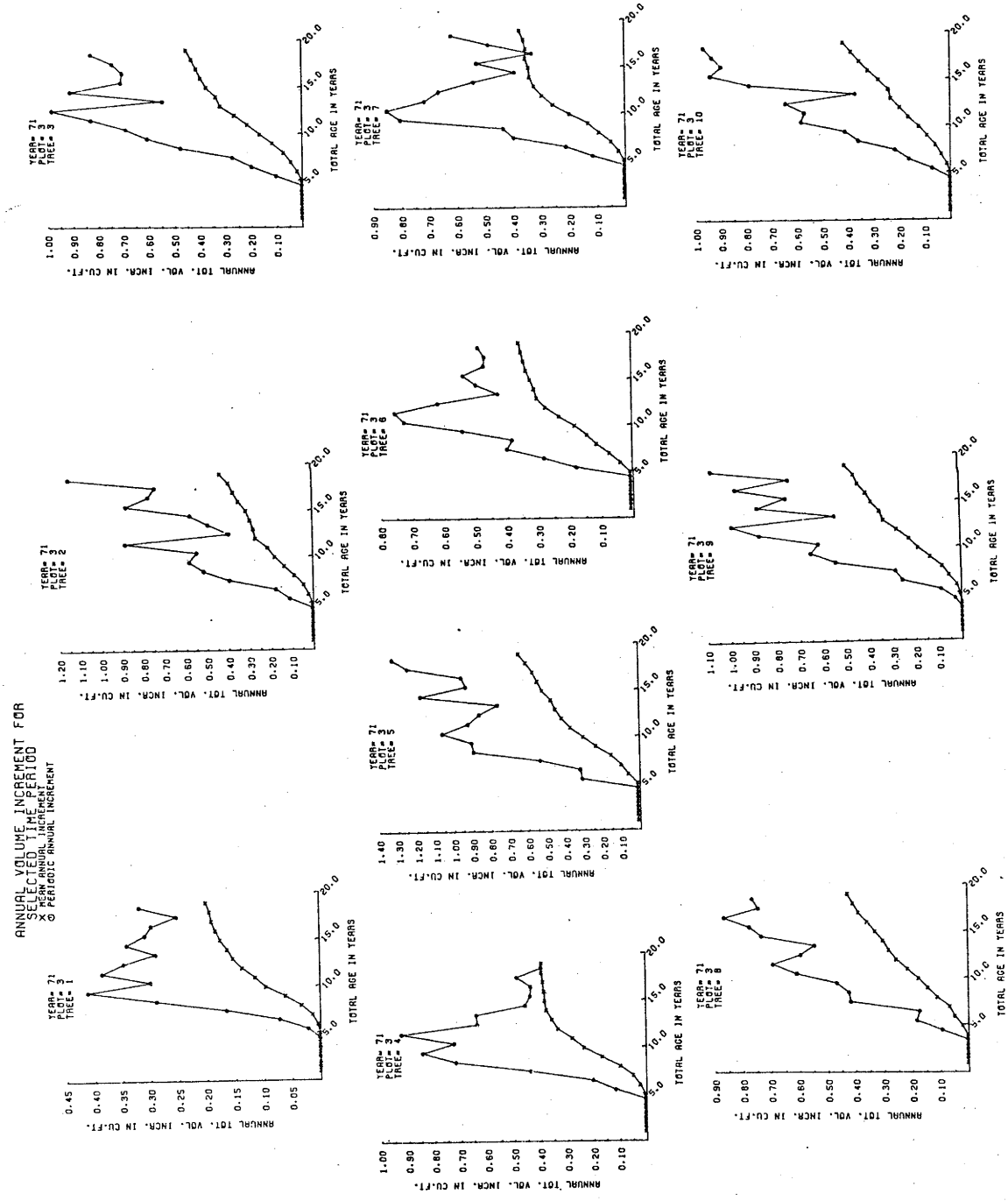


Figure A.7(c): Danbulla.

APPENDIX 4

WEIGHTED VALUES OF SEVEN DENSITOMETRIC CHARACTERS IN INDIVIDUAL TREES

In this Appendix are presented the weighted disc average values at breast height and percentile height levels and the weighted whole-tree average value of the ring maximum density (Table A5), minimum density (A6), mean density (A7), density range (A8), latewood percentage (A9), width of the intraincremental latewood zone (A10), and latewood ratio (A11), in each of the 20 trees of the Beerburrum sub-plots A and B. The mean tree value and standard deviation at each height level is indicated. The system of weighting is described in Section 4.4.

Table A.5 Ring Maximum Density

Tree number	Weighted average value						
	(a). at percentile height levels						(b).whole-tree
	breast height	10%	20%	40%	60%	80%	
A.1	.987	1.035	.942	.844	.878	.675	.914
A.2	.947	.850	.891	.825	.845	.819	.870
A.3	.936	.928	.947	.857	.807	.931	.899
A.4	.703	.601	.617	.566	.629	.621	.618
A.5	.775	.772	.795	.714	.759	.810	.764
A.6	.942	.925	.759	.676	.763	.603	.780
A.7	.878	.877	.816	.785	.857	.784	.829
A.8	.913	.931	.936	.770	.743	.765	.847
A.9	.916	.881	.792	.769	.805	.599	.813
A.10	.756	.814	.719	.637	.569	.587	.694
B.1	.727	.693	.639	.607	.659	.628	.657
B.2	.761	.770	.705	.710	.739	.669	.729
B.3	.941	.992	.953	.932	.884	.876	.937
B.4	.800	.768	.745	.696	.492	.653	.713
B.5	.925	.886	.866	.806	.822	.919	.860
B.6	.738	.769	.666	.672	.656	.534	.685
B.7	.808	.839	.796	.802	.652	.618	.774
B.8	.920	.885	.825	.788	.833	.908	.846
B.9	.976	.947	.951	.976	.981	.893	.961
B.10	.830	.869	.854	.705	.607	.617	.762
mean tree value	.859	.852	.811	.757	.749	.725	.798
s.d.	.092	.103	.107	.104	.123	.131	.096

Table A.6 Ring Minimum Density

Tree number	Weighted average value						
	(a). at percentile height levels						(b).whole-tree
	breast height	10%	20%	40%	60%	80%	
A.1	.335	.352	.323	.316	.331	.336	.329
A.2	.359	.350	.344	.335	.343	.348	.345
A.3	.328	.344	.337	.332	.335	.337	.335
A.4	.332	.310	.301	.311	.322	.329	.315
A.5	.355	.351	.325	.337	.352	.342	.342
A.6	.342	.334	.311	.309	.311	.332	.319
A.7	.388	.373	.349	.356	.376	.353	.364
A.8	.374	.377	.367	.350	.338	.311	.357
A.9	.420	.419	.397	.383	.363	.329	.393
A.10	.383	.400	.349	.366	.362	.332	.367
B.1	.351	.325	.332	.320	.342	.325	.332
B.2	.336	.324	.319	.320	.312	.341	.323
B.3	.352	.337	.338	.331	.321	.339	.336
B.4	.352	.332	.329	.334	.300	.353	.332
B.5	.396	.382	.368	.356	.361	.379	.371
B.6	.358	.345	.312	.318	.323	.333	.327
B.7	.327	.317	.322	.309	.318	.318	.318
B.8	.389	.366	.379	.347	.344	.360	.365
B.9	.438	.422	.407	.414	.418	.394	.417
B.10	.372	.389	.368	.357	.332	.342	.361
mean tree value	.364	.357	.344	.340	.340	.342	.347
s.d.	.031	.033	.029	.027	.027	.020	.027

Table A.7 Ring Mean Density

Tree number	Weighted average value (a). at percentile height levels						(b).whole-tree
	breast height	10%	20%	40%	60%	80%	
A.1	.536	.579	.496	.466	.469	.452	.500
A.2	.575	.497	.518	.470	.455	.434	.501
A.3	.584	.516	.532	.484	.464	.448	.514
A.4	.478	.414	.395	.393	.407	.424	.414
A.5	.520	.499	.493	.431	.457	.429	.473
A.6	.515	.511	.448	.431	.462	.434	.463
A.7	.563	.556	.549	.547	.536	.475	.544
A.8	.548	.610	.585	.473	.443	.415	.520
A.9	.564	.564	.549	.546	.472	.491	.540
A.10	.546	.558	.510	.455	.454	.468	.501
B.1	.466	.469	.434	.427	.460	.400	.445
B.2	.506	.481	.446	.436	.425	.479	.457
B.3	.555	.548	.543	.471	.462	.524	.515
B.4	.495	.500	.442	.450	.384	.471	.456
B.5	.565	.571	.576	.495	.479	.491	.538
B.6	.541	.493	.447	.406	.400	.429	.450
B.7	.460	.493	.452	.430	.421	.416	.447
B.8	.558	.559	.516	.523	.511	.493	.528
B.9	.618	.612	.581	.606	.577	.530	.594
B.10	.570	.568	.519	.508	.419	.437	.509
mean tree value	.538	.529	.502	.472	.458	.457	.495
s.d.	.041	.050	.055	.053	.046	.037	.044

Table A.8 Ring density Range

Tree number	Weighted average value						
	(a). at percentile height levels						(b).whole-tree
	breast height	10%	20%	40%	60%	80%	
A.1	.652	.682	.619	.528	.546	.339	.585
A.2	.588	.499	.547	.490	.502	.470	.524
A.3	.608	.584	.610	.525	.472	.593	.564
A.4	.371	.291	.316	.255	.307	.292	.303
A.5	.421	.421	.469	.377	.407	.468	.422
A.6	.600	.591	.449	.367	.453	.271	.461
A.7	.490	.503	.466	.430	.482	.432	.465
A.8	.539	.554	.569	.420	.405	.455	.491
A.9	.496	.462	.395	.386	.442	.271	.420
A.10	.373	.415	.369	.271	.207	.255	.327
B.1	.376	.369	.307	.288	.316	.302	.324
B.2	.425	.446	.386	.390	.427	.328	.406
B.3	.589	.655	.616	.601	.563	.536	.601
B.4	.448	.437	.416	.363	.193	.300	.381
B.5	.528	.503	.498	.450	.460	.539	.488
B.6	.380	.424	.354	.354	.332	.201	.357
B.7	.480	.521	.474	.494	.334	.300	.456
B.8	.531	.520	.445	.441	.488	.548	.481
B.9	.537	.526	.544	.562	.563	.498	.544
B.10	.458	.480	.487	.348	.275	.275	.401
mean tree value	.494	.494	.467	.417	.409	.384	.450
s.d.	.087	.093	.096	.096	.111	.120	.087

Table A.9 Latewood Percentage

Tree number	Weighted average value						
	(a). at percentile height levels						(b).whole-tree
	breast height	10%	20%	40%	60%	80%	
A.1	46.57	50.34	37.57	30.14	24.98	28.76	36.79
A.2	50.42	37.23	42.01	29.92	22.22	26.06	36.44
A.3	41.68	43.96	44.18	37.02	25.89	22.72	38.36
A.4	33.08	19.24	16.59	11.74	11.94	12.13	17.28
A.5	45.06	45.97	36.28	28.93	29.12	20.97	34.99
A.6	45.34	37.10	24.59	15.67	19.23	23.32	26.14
A.7	57.29	50.10	42.65	43.97	45.00	26.93	45.29
A.8	59.63	57.48	52.39	34.93	19.50	14.42	41.79
A.9	71.21	65.27	57.65	55.09	38.75	25.83	56.60
A.10	60.05	63.70	47.52	34.24	20.51	16.91	43.98
B.1	34.00	27.74	26.46	15.37	23.78	20.89	24.70
B.2	36.47	29.87	26.00	23.75	18.61	16.82	26.68
B.3	48.55	48.53	42.86	33.83	26.91	28.06	39.40
B.4	39.59	32.68	32.67	24.42	3.45	25.18	28.07
B.5	58.34	54.89	44.08	29.61	24.98	29.66	41.62
B.6	36.63	36.03	24.62	17.64	7.57	5.77	22.97
B.7	32.01	26.89	28.88	24.20	10.72	7.06	24.16
B.8	54.80	47.38	53.55	35.18	32.38	36.15	44.33
B.9	75.30	67.39	64.37	64.77	57.22	42.31	64.32
B.10	54.37	59.95	48.86	37.10	24.72	13.06	42.37
mean tree value	49.02	45.09	39.69	31.38	24.38	22.15	36.81
s.d.	12.34	13.93	12.62	12.96	12.50	9.17	11.68

Table A.10 Width (mm) of the Intraincremental Latewood Zone

Tree number	Weighted average value						
	(a). at percentile height levels						(b).whole-tree
	breast height	10%	20%	40%	60%	80%	
A.1	3.70	3.63	2.81	2.60	2.35	3.11	2.98
A.2	4.41	3.20	3.61	2.65	2.08	2.86	3.22
A.3	3.62	3.54	3.50	3.17	2.74	2.17	3.28
A.4	2.03	1.14	0.94	0.81	0.89	1.17	1.11
A.5	2.55	2.72	2.11	1.89	2.24	1.99	2.22
A.6	2.50	2.19	1.50	0.91	1.32	2.01	1.58
A.7	2.78	2.47	1.99	2.73	3.53	2.13	2.63
A.8	2.86	2.72	2.51	1.71	1.16	1.05	2.07
A.9	2.28	1.93	1.82	1.78	1.23	1.21	1.81
A.10	2.65	2.92	2.21	1.24	1.08	1.05	1.96
B.1	3.05	2.24	2.20	1.43	2.99	2.22	2.26
B.2	3.15	2.50	2.09	2.40	2.41	1.76	2.45
B.3	3.51	3.43	2.96	2.68	2.71	2.79	3.01
B.4	2.59	2.05	2.19	1.76	0.32	2.38	1.91
B.5	3.65	3.78	2.79	2.32	2.40	3.48	2.94
B.6	1.91	1.79	1.39	1.06	0.90	0.49	1.33
B.7	1.76	1.45	1.51	1.43	0.85	0.63	1.38
B.8	2.83	2.21	2.66	1.82	2.06	3.59	2.40
B.9	2.90	2.55	2.12	2.16	2.21	2.25	2.35
B.10	1.54	1.85	1.27	1.04	0.68	0.71	1.20
mean tree value	2.81	2.52	2.21	1.88	1.81	1.95	2.20
s.d.	0.73	0.74	0.71	0.69	0.89	0.93	0.67

Table A.11 Latewood Ratio

Tree number	Weighted average value						
	(a). at percentile height levels						(b).whole-tree
	breast height	10%	20%	40%	60%	80%	
A.1	.315	.335	.289	.301	.262	.363	.303
A.2	.368	.300	.323	.271	.239	.174	.297
A.3	.434	.301	.329	.298	.275	.202	.323
A.4	.415	.382	.288	.345	.300	.324	.338
A.5	.413	.357	.362	.266	.266	.208	.320
A.6	.302	.316	.343	.335	.327	.401	.331
A.7	.373	.371	.438	.446	.345	.331	.399
A.8	.336	.431	.402	.301	.282	.263	.341
A.9	.299	.326	.410	.458	.247	.603	.378
A.10	.440	.402	.428	.343	.509	.545	.423
B.1	.321	.412	.344	.405	.356	.290	.364
B.2	.434	.376	.363	.326	.251	.443	.356
B.3	.352	.328	.344	.256	.262	.338	.308
B.4	.329	.401	.266	.326	.404	.427	.335
B.5	.338	.390	.441	.340	.298	.211	.365
B.6	.499	.345	.389	.256	.229	.486	.349
B.7	.276	.341	.264	.258	.322	.339	.287
B.8	.332	.396	.310	.399	.353	.259	.349
B.9	.344	.373	.341	.349	.303	.290	.339
B.10	.451	.364	.327	.458	.326	.360	.387
mean tree value	.369	.362	.350	.337	.308	.343	.345
s.d.	.061	.037	.054	.066	.066	.116	.035

Table 4.1: Identification of wood character variables.

Reference	Wood character
1	Maximum density (DMAX)
2	Minimum density (DMIN)
3	Mean density (DEN)
4	Density range (DR)
5	Ring width (RWID)
6	Latewood percentage (% LW)
7	Latewood width (radial width - mm) (LWID)
8	Latewood ratio (LR)
9	Latewood cell wall thickness (LWW)
10	Latewood cell lumen diameter (LWL)
11	Earlywood cell wall thickness (EWW)
12	Earlywood cell lumen diameter (EWL)
13	Latewood cell diameter (LWCD)
14	Earlywood cell diameter (EWCD)
15	Tracheid length (LFIB)